The 1994 Stellako River Sockeye Salmon *(Oncorhynchus nerka)* Escapement: Evaluation of Pooled Petersen and Stratified Mark-Recapture Estimates of a Known Population

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ABSTRACT

Schubert, N.D. 2000. The 1994 Stellako River sockeye salmon (*Oncorhynchus nerka*) escapement: evaluation of pooled Petersen and stratified mark-recapture estimates of a known population. Can. Tech. Rep. Fish. Aquat. Sci. 2303: 56 p.

Mark-recapture studies have been the standard tool for estimating the escapement of large Fraser River sockeye populations since the 1940's. The accuracy of these estimates depends on how well the assump-tions underlying the technique are met. Most studies address the assumptions by developing rigorous study designs, testing the data for bias, and selecting the most appropriate estimate from pooled and stratified data. Two weaknesses in this approach are that estimation accuracy cannot be examined because the true population size is unknown, and rigorous procedures have not been developed to identify the conditions under which the stratified estimate should be adopted. The installation of a counting fence on the Stellako River provided an opportunity to evaluate these weaknesses in a mark-recapture study of a major Fraser River sockeye stock. The objectives of the study were to: update the historic escapement database for Stellako River sockeye; compare the accuracy of mark-recapture estimates generated from recovery data col-lected on the spawning grounds and at the enumeration fence; determine whether stratification and selective pooling improve estimation accuracy; and develop rules for choosing the most appropriate population esti-mator and the most accurate population estimate.

A total of 121,525 sockeye were counted through the enumeration fence. The study area population, estimated from the fence count (121,525), a visual survey of the river on the day the fence was installed (13,050), and adjusted for emigration to upstream spawning areas, was 134,377. Petersen disk tags were applied to 1,225 sockeye as they migrated through the fence. Carcasses were examined for tags as they were recovered on the spawning grounds or washed downstream against the fence; 82,552 carcasses were recovered, of which 679 had disk tags.

The pooled Petersen estimates (PPE) had errors ranging from -1% to +18% of the true population size. Estimation error resulted from a lower probability of recovery of tagged versus untagged sockeye, with different mechanisms affecting each sex. Among males, handling stress may have impaired the abil-ity of tagged fish to migrate further upstream and caused an earlier death. Among females, several fact-ors (tag loss, predator removal, and the failure of technicians to recognize tagged fish) in combination with the effects of subacute stress may have reduced the recoverability of tagged fish. The evaluation of strati-fied population estimators concluded that: a) the Schaefer estimator will not substantially improve the accuracy of a PPE and should be abandoned for use in population estimation; and b) the maximum likeli-hood Darroch estimator can potentially increase the accuracy of the PPE, but its use should be suspended pending mathematical developments to adapt it to species such as sockeye where mixing of tags across recovery strata is common. In the interim, the PPE should be adopted as the sole population estimator, with alternate procedures developed to permit the qualitative and, ultimately, quantitative evaluation of bias.

RÉSUMÉ

Schubert, N.D. 2000. The 1994 Stellako River sockeye salmon (*Oncorhynchus nerka*) escapement: evaluation of pooled Petersen and stratified mark-recapture estimates of a known population. Can. Tech. Rep. Fish. Aquat. Sci. 2303: 56 p.

Les études basées sur le marquage et la recapture sont utilisées depuis les années 1940 pour estimer l'échappée des grandes populations de saumons rouges du Fraser. La précision de ces estimations dépend de certaines conditions qui doivent être remplies pour que la technique puisse être appliquée. Dans la plupart des cas, les spécialistes s'efforcent de remplir ces conditions en mettant au point des plans d'étude rigoureux, en vérifiant la présence éventuelle de biais dans les données et en choisissant l'estimation la plus appropriée à partir des données groupées et à partir des données stratifiées. Cette approche a deux inconvénients : 1) il est impossible d'évaluer la précision de l'estimation parce que la taille réelle de la population est inconnue; 2) aucune procédure rigoureuse n'a été développée pour identifier les conditions dans lesquelles l'estimation basée sur l'échantillon stratifié devrait être adoptée. L'installation d'une barrière de dénombrement sur la rivière Stellako a permis d'évaluer l'effet de ces inconvénients lors d'une étude basée sur le marquage et la recapture d'un important stock de saumons rouges du Fraser. Les objectifs de l'étude étaient de : 1) mettre à jour la base de données décrivant l'échappée des saumons rouges de la rivière Stellako; 2) comparer la précision des estimations basées sur le marquage et la recapture entre les données issues des décomptes sur les frayères et les données issues du décompte à la barrière de dénombrement; 3) déterminer si la stratification et le groupage sélectif améliorent la précision de l'estimation; 4) élaborer des règles permettant de choisir l'estimateur de population le plus approprié et donc d'effectuer l'estimation la plus précise possible de la population.

On a dénombré un total de 121 525 saumons rouges à la barrière de dénombrement. La population du secteur étudié, estimée à partir du dénombrement à la barrière (121 525), d'un recensement aérien de la rivière le jour de l'installation de la barrière (13 050) et d'un ajustement visant à rendre compte de la migration vers les frayères situées en amont, s'élève à 134 377 saumons. Des disques de Petersen ont été attachés à 1 225 saumons rouges lors de leur passage par la barrière de dénombrement. On a examiné les carcasses présentes sur les frayères ou accumulées sur la barrière, en aval, pour y déceler la présence éventuelle d'une marque; on a récupéré 82 552 carcasses dont 679 portaient un disque.

L'erreur associée aux estimations effectuées par la méthode de l'estimateur multiple de Petersen variait entre -1% et +18% de la taille réelle de la population. L'erreur de l'estimation provenait d'une probabilité moindre de retrouver les saumons rouges marqués, comparativement aux saumons non marqués, avec des mécanismes de perturbation différents suivant le sexe. Parmi les mâles, le stress dû à la manipulation a pu affecter la capacité des poissons marqués de remonter plus en amont, causant la mort prématurée de ces spécimens. Chez les femelles, plusieurs facteurs (perte de la marque, attaque du poisson par les prédateurs et non comptage accidentel par les techniciens) combinés aux effets d'un stress subaigu ont pu diminuer la possibilité de retrouver les spécimens marqués. L'examen des estimateurs de population stratifiée a permis de conclure que : a) l'estimateur de Schaefer ne permet pas d'améliorer de manière significative la précision de la méthode de l'estimateur multiple de Petersen et il ne doit plus être utilisé pour l'estimation de la taille des populations; b) l'estimateur de probabilité maximum de Darroch peut permettre d'augmenter la précision de la méthode de l'estimateur multiple de Petersen mais son utilisation doit attendre la conclusion d'une étude mathématique visant à l'adapter à des espèces telles que le Saumon rouge pour lesquelles le mélange des marques entre les strates de récupération est chose commune. En attendant, la méthode de l'estimateur multiple de Petersen doit être adoptée comme seule méthode acceptable d'estimation de population tandis que d'autres procédures sont mises au point pour effectuer une analyse qualitative, et finalement quantitative, des biais statistiques.

INTRODUCTION

The Fraser River system supports the largest population of sockeye *salmon (Oncorhynchus nerka*) in the world (Northcote and Larkin 1989). Sockeye spawn in over 150 natal areas, ranging from small streams to large rivers and lakes, which are distributed throughout the accessible portion of the Fraser system. Since 1938, escapements have been monitored using procedures developed by the International Pacific Salmon Fisheries Commission. Mark-recapture studies, developed from the pioneering work of Howard (1948) and Schaefer (1951) in the Cultus and Harrison systems, respectively, are now broadly used to estimate the escapement of larger (25,000+ spawners) sockeye stocks.

Mark-recapture studies are based on the principle that, by tagging a random sample of fish, permitting them to redistribute through the population, and obtaining a second random sample of tagged and untagged individuals, the number of fish in the population can be estimated with known precision. The accuracy of the resulting estimate, however, depends on whether the assumptions underlying the technique have been met. These assumptions have been described in various forms by Ricker (1975), Otis *et al.* (1978), Eames *et al.* (1981), and Seber (1982). Most mark-recapture studies address the assumptions by developing rigorous study designs, testing the data for bias, and comparing the estimates from pooled and stratified data (e.g. Schubert and Fanos (1997)). These procedures permit the detection and correction of study deficiencies and may mitigate the impact of assumption violations on the population estimates.

Two weaknesses of this approach are that estimation accuracy cannot be examined because the true population size is unknown, and rigorous procedures have not been developed to identify the conditions under which the stratified estimate should be adopted. A new generation of computer software (e.g. the Stratified Population Analysis System (Arnason *et al.* (1996)) now permits the experimenter to address assumption violations by using maximum likelihood and other stratified estimators to easily generate a large number of population estimates under a variety of pooling scenarios. Its current application is limited, however, because decision rules have not been developed to select among the stratified estimates or between the stratified and pooled Petersen estimates. What is needed, then, is an opportunity to evaluate bias in mark-recapture estimates for a population whose size is known. This will allow an evaluation of the accuracy of the pooled Petersen estimator, the standard analytic tool for Fraser River sockeye studies since the 1940's, and the development of decision rules for the selection of the most appropriate, least biased population estimator.

The Stellako River provides such an opportunity for a major Fraser River sockeye stock. As a short inter-lake river with stable flows and a well-defined channel, the Stellako is an ideal site for a reliable, relatively low cost, temporary enumeration fence. The installation of a fence in 1994 permitted the daily enumeration of sockeye into the study area and the application of tags to a known proportion of the population. The study had four broad objectives: to update the historic escapement database by providing a best estimate of the Stellako River sockeye escapement; to evaluate the accuracy of mark-recapture estimates generated for a component of the population (the mark-recapture "study area"); to determine whether stratification and selective pooling improve estimation accuracy; and to develop rules for choosing the most accurate population estimate.

In this report, I describe the study design, field methods, analyses and results for the visual, enumeration fence and mark-recapture components of the 1994 study. I provide the most accurate estimates of escapement by age and sex, and present mark-recapture results relative to that estimate. I evaluate the role of stress in estimation error, and investigate rules for choosing the most accurate maximum likelihood estimate, and for choosing between that estimate and the pooled Petersen estimate. I conclude with a discussion of the implication of the results to the analysis of mark-recapture data in general and the design of future Stellako River studies in particular.

STUDY AREA

The Stellako River is part of the Nechako River System, which comprises the northwest portion of the Fraser River watershed (Fig. 1). The system supports two temporally and spatially distinct sockeye stocks, a small early summer run and a larger summer run. The early summer run migrat-

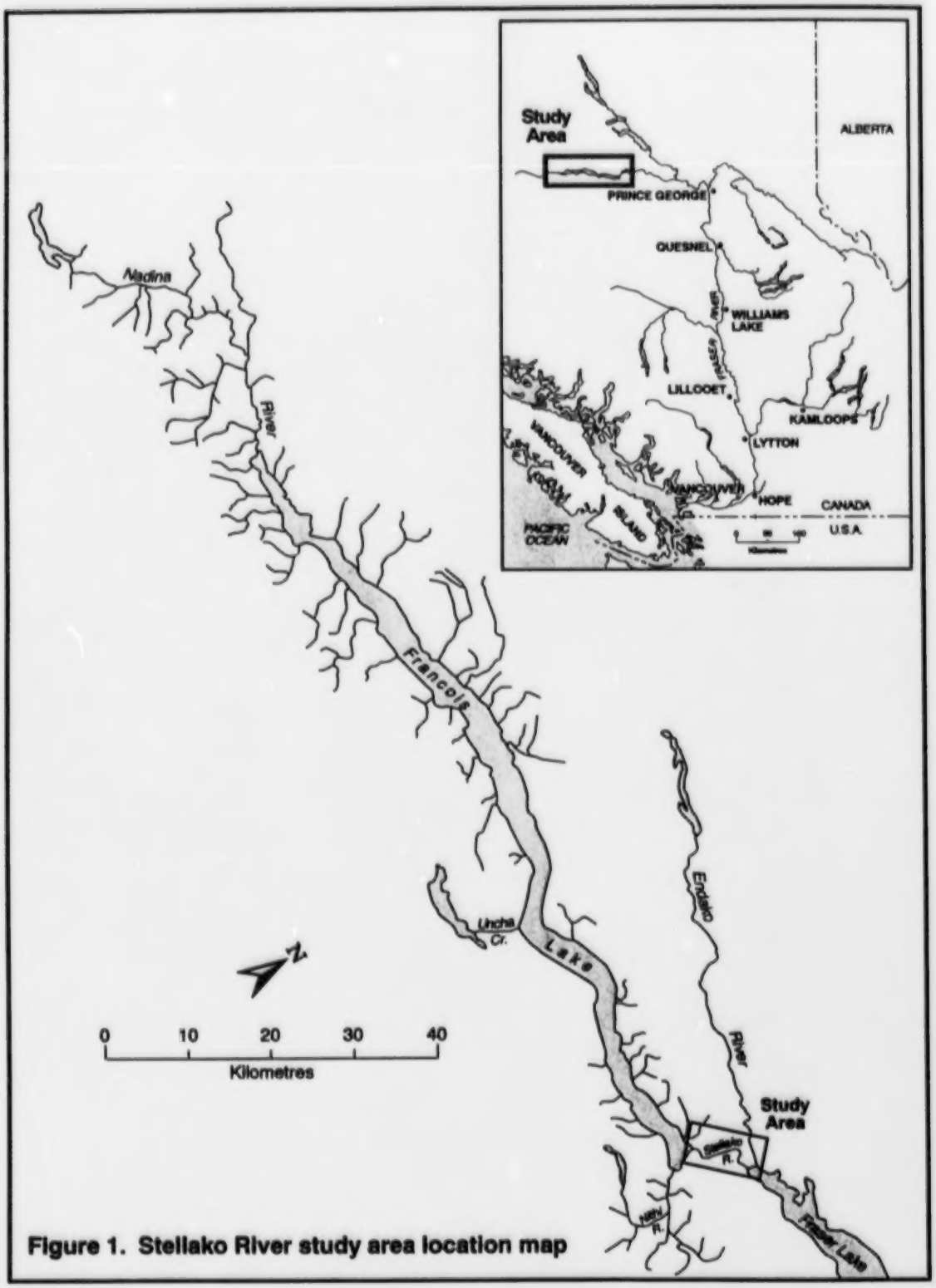

Figure 1. Stellako River study area location map

es through the Stellako River from mid-July to late August and spawns in the Nadina and Nithi rivers. The estimation of the 1994 escapement of these stocks is described by Schubert (1998). The summer run arrives in the Nechako River from late August to late September and spawns in the Nechako and Stellako rivers. The assessment of the former is described by Schubert (1998); the latter is the focus of this report. Like most summer run Fraser River sockeye stocks, Stellako escapements collapsed after the Hell's Gate slide and remained at very low levels until rebuilding began in 1938 (Anon. 1966). Early in the rebuilding period, the 1938-1966 cycle was dominant (Appendix 1); however, subsequent escapements have not exhibited a pronounced quadrennial cycle. Escapements have generally increased, from an average of 70,000 in the 1950's and 1960's to an average of over 90,000 since 1970 (Appendix 1).

The Stellako River arises at Francois Lake and flows northeast for 13 km, entering the west end of Fraser Lake (Fig. 1). The river has a generally shallow, well defined, and stable channel with a bouldery substrate. Coniferous trees and shrubs grow to the high water mark, and fallen trees commonly enter the river from the shore. Daily discharges (1951-1990) averaged 21 m^3s^{-1}, with mean daily minima (7 m^3s^{-1}) and maxima (62 m^3s^{-1}) occurring in March and June, respectively (Environment Canada 1991). The river was divided into nine areas loosely based on the homogeneity of physical characteristics (Fig. 2). These areas facilitated the aggregation of data for bias testing and the use of stratified models, and were the same as those used since 1942 (Anon. 1966). I briefly describe each area below.

Area 1 (1.7 km in length) is the uppermost section of the Stellako River. The river flows in rapids and riffles separated by isolated pools and runs. The channel is 35 m wide and has a relatively high gradient and a substrate of boulder and cobble; gravel bars and beaches are rare.

Area 2 (1.1 km), which extends from a bedrock chute to a wing dam formerly used during log drives, has a lower gradient and a wider (60 m) channel than in Area 1. A 30 m high canyon wall confines the channel to the north as the river flows in long, shallow runs separated by riffles and rapids. The substrate is largely boulders and sand, with scattered sections of small gravel.

Area 3 (0.8 km), which extends downstream to another bedrock chute, has a higher gradient a 25-35 m wide channel, and low valley walls (10 m) that slope away from the river. The river flows in a series of rapids and shallow runs and has a substrate of boulder and cobble.

In Area 4 (0.7 km), the channel is sinuous and is confined by a high bedrock wall on the south shore. The gradient is higher in the upper part of the area, resulting in frequent rapids and a cobble substrate. This changes to a lower gradient with long runs and a gravel substrate.

Area 5 (0.5 km) begins at the "big eddy", a 60 m wide, deep pool which forms where the river turns sharply around a high bedrock outcrop. Below the pool, the gradient is low and the river has a width of 30 m and is characterised by long, deep pools and runs and a substrate of small gravel.

In Area 6 (1.8 km), which extends downstream to a 1.5 m high falls, the river has a moderate gradient and flows in a series of rapids, riffles and shallow runs. The channel has low, stable banks, and the valley walls are set well back from the river. The substrate is cobbles and boulders.

In areas 7 (2.4 km) and 8 (0.6 km), the river is more sinuous, with discrete gravel bars at meanders in the channel. In the upper part of Area 7, the gradient is moderate and the river is characterized by rapids and riffles and a boulder-cobble substrate. Downstream, the river flows in a series of riffles and runs and has a gravel substrate. Bank erosion occurs along isolated grassy benches.

Area 9 (0.8 km), which extends from an area known as "grassy banks" to a lagoon near the river mouth, is similar to Area 8 except the channel is wider and less confined, and the river braids around gravel bars. In the lower 0.5 km (below the enumeration fence), the river flows across a marshy lowland where the channel is braided and has low grassy banks and an unstable sandy substrate. Bank erosion occurs throughout Area 9. Below Area 9, the river enters a vegetation-filled lagoon before flowing through a deep, slow moving channel into Fraser Lake. The Endako River enters the Stellako River at the lagoon. Historically, the Endako supported sockeye spawners; however, none have been reported since 1990.

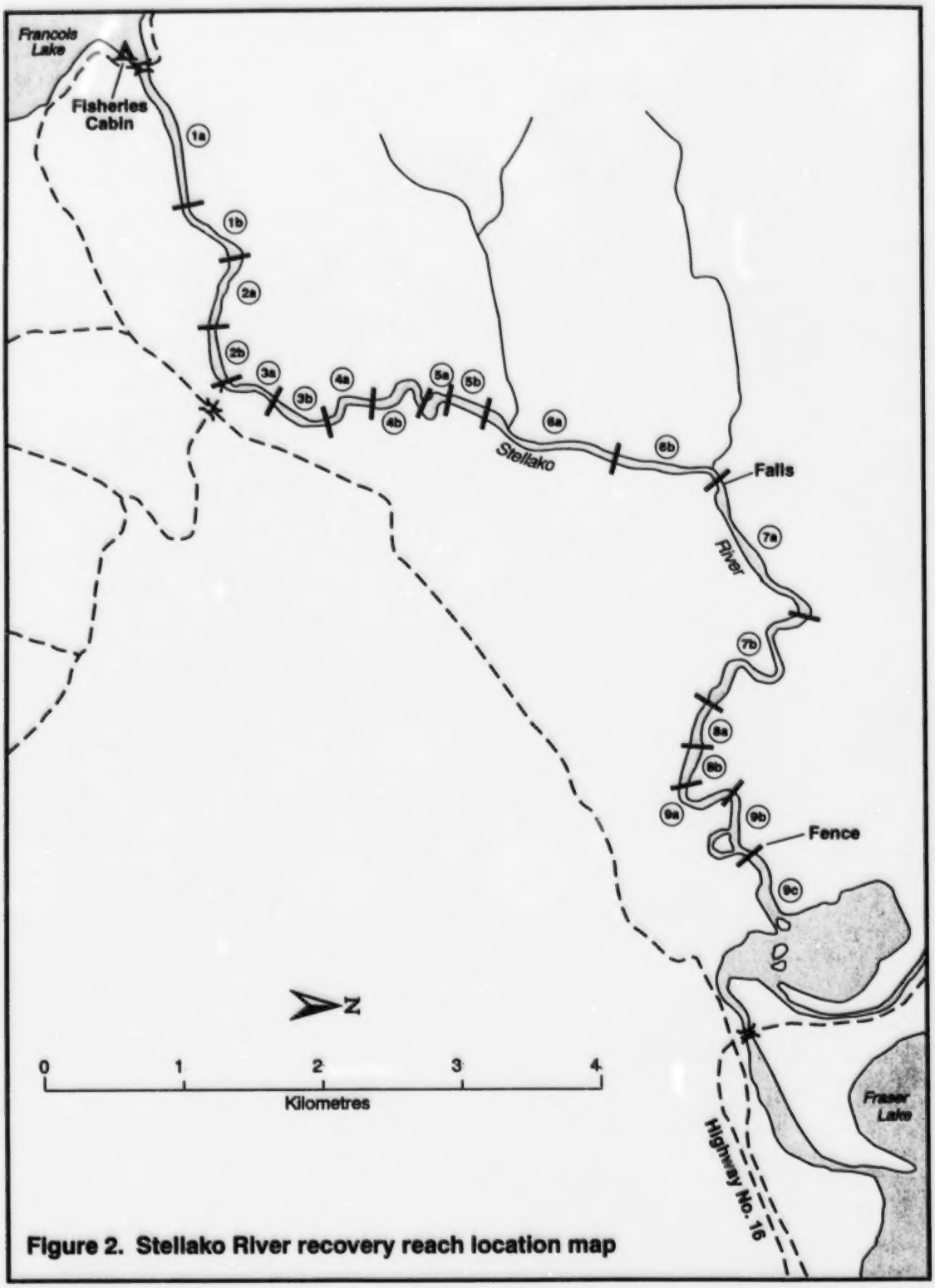

Figure 2. Stellako River recovery reach location map

FIELD METHODS

VISUAL SURVEYS

The river was surveyed by boat on the day the fence was completed. One person operated the boat while another counted live sockeye from an elevated platform. Similar surveys were conducted periodically below the fence after spawning (rather than migrating) sockeye were first observed in that area.

ENUMERATION FENCE

An enumeration fence was constructed in the lower Stellako River approximately 0.5 km upstream from the lagoon (Fig. 2). The fence consisted of two wings aligned in an upstream "V", with a 2 m x 2 m white-bottomed box at the apex. A platform and halogen lamp adjacent to the box permitted continuous observation. The fences and box were constructed from 2.3 cm diameter, 1.8 m long wooden broom sticks inserted through holes drilled at 3.8 cm intervals in two aluminium stringers. The stringers were secured to the substrate with 3 m long angle iron supports. Chicken wire attached to additional supports which projected above the fence prevented fish from jumping the fence. The substrate under the fence was protected from erosion by an 1 m wide apron of plastic coated chain-link fencing wrapped in 6 mm plastic sheeting. Sandbags lined the ends and both sides of the fence and the base of the supports.

When fish were observed pooling below the fence, several broomsticks were removed from the ends of the box to permit fish to swim through the box. Observations were recorded by date, hour, number, species and direction of travel; sex was not recorded because the identification of sex in live, moving salmon is unreliable. Sockeye were trapped for sampling and tagging by replacing the broomsticks at the upstream end of the box. Drifting carcasses were removed from and thrown into the river below the fence; these carcasses did not receive an identifying mark.

MARK-RECAPTURE

Tag Application

Daily tagging targets were set at 1% of the previous day's total sockeye migration past the fence. The fish were dip netted from the trap box and transferred to a holding pen where they were held until a tagger was available. Sockeye that were damaged were released untagged. The remaining fish were removed from the pen and marked with Petersen disk tags. The fish were tagged in a wooden tray (12 cm x 20 cm x 100 cm) constructed with a flexible plastic bottom and a metre stick recessed in one side; the tray was set in a stand elevated above the water surface. The tags consisted of two red 15-mm diameter laminated cellulose acetate disks threaded through centrally punched holes onto a 77 mm long nickel pin. The pin was inserted with pliers through the musculature and pterygiophore bones approximately 12 mm below the anterior portion of the dorsal fin insertion. The disk tags, arranged with one on each side of the fish, were secured by twisting the pin into a double knot. One disk per pair was numbered with a unique code. Date of capture, disk tag number, nose-fork length, sex (fish with length less than 50 cm were recorded as jacks), and marks (troll, gill net, and lamprey scars) were recorded for each fish released with a disk tag. Condition at release was recorded as 1 (swam away vigorously), 2 (swam away sluggishly) or 3 (required ventilation).

Spawning Ground Surveys

Main Survey: The survey was designed to achieve equal recovery probabilities for carcasses washing ashore in all parts of the study area. The surveys were conducted on a two-day cycle for the duration of the die-off, with all known spawning areas surveyed each cycle. The surveys began after the first carcasses were observed near the fence and continued until the die-off was virtually complete. The shores were surveyed on foot by two-person crews using an inflatable boat to leapfrog down the river; up to three crews were required at the peak of die-off.

The crews were trained to recover carcasses independent of their tag status and, following recovery, to place a higher priority on the correct identification of tag status than on survey speed. All carcasses that were on shore or retrievable with a peough by wading into the river to knee depth were enumerated and thrown on the bank above the high water mark. The carcasses were recorded by date, reach, sex, tag status, carcass condition (fresh, tainted or rotten) and female spawning

success (0%, 50% or 100% spawned). If a disk tag was present, it was retrieved and the tag number was recorded before the carcass was processed.

Resurvey: Previously processed carcasses were resampled through the recovery period to estimate the number of tagged carcasses whose tag status had not been identified correctly. The resurvey, conducted by an experienced technician, recorded carcasses by date, area, sex and tag status. If a disk tag was present, it was retrieved and recorded as noted above.

BIOLOGICAL SAMPLING

Biological samples were obtained following a protocol provided by the Pacific Salmon Commission. Adult sockeye were sampled for postorbital-hypural plate (POH) and nose-hypural plate (standard) lengths, otoliths and scales (one from each preferred region, as defined by Clutter and Whitesel (1956)). Sixty carcasses of each sex were sampled in the Stellako River ten days before (based on the historic mean date), during, and ten days after the peak die-off. All recovered jacks were sampled for scales and lengths.

Fifty females, killed during the peak of arrival at the enumeration fence, were similarly sampled and the egg skeins and loose eggs were removed, placed in a cotton bag and preserved in a 10% formaldehyde solution. I estimate the number of eggs in each sample as the product of the total skein weight and the number of eggs per gram in a weighed sub-sample of the skein, plus a count of the loose eggs.

ANALYTIC PROCEDURES

ESCAPEMENT ESTIMATE

I use the visual and fence observations to estimate the sockeye escapement in two overlapping but distinct areas: the mark-recapture study area, and the entire Stellako River. The former (hereafter, the "study area") consists of the Stellako River above the enumeration fence. Because this population was also assessed by the mark-recapture study, this estimate provides a benchmark against which the accuracy of the mark-recapture estimates can be determined. The latter (hereafter, the "Stellako River") includes the area below the fence. This is the area that has been assessed annually since 1938; consequently, the Stellako River estimate updates the historic escapement database (Appendix 1).

The study area escapement is estimated from three data sources: the fence count; an estimate of the number of sockeye counted at the fence that did not spawn in the Stellako River (Nadina sockeye); and an estimate of the number of Stellako River spawners present in the river before the fence was installed. The Stellako River escapement consists of the above plus an estimate of the number of sockeye that spawned below the fence. Each component is described in more detail below.

The fence censused the population that entered the Stellako River from August 31 until the run was complete; however, some of those fish were from the relatively small Nadina stock that immigrated earlier in the summer. That population is estimated from the ratio of the disk tags recovered in a census of the Nadina escapement and the average tag rate at the fence; those fish are then subtracted from the fence count. I partition the remainder (the Stellako spawners) into males, females and jacks based on the proportion of each (jacks adjusted by 1.26 using the IPSFC procedure (Andrew and Webb MS 1987)) in the complete carcass recovery sample.

I use visual observations to estimate the population of sockeye that were already in the upper river when the fence was installed (because these fish were holding in pools rather than migrating, I assume they were not *en route* to Nadina). The sum of the live spawner count and the cumulative carcass recovery to the date of the live count is adjusted by an index expansion factor (1.8) developed by the IPSFC (based on comparisons of visual data with mark-recapture and enumeration fence estimates (Woodey 1984)). Again, I partition the estimate by sex based on the proportions in the complete adult carcass sample.

The escapement below the fence is estimated from visual surveys and estimated spawner residence time using "area under the curve" software (Irvine *et al.* (1993). Migratory fish are excluded by subtracting from each observation the fence count for the following two days. Residence time is the time between tagging and spawning ground recovery for sockeye tagged after spawning was first observed below the fence.

MARK-RECAPTURE STUDY

Three recovery data sets are used to calculate the population estimates: spawning ground (comparable to a study with frequent spawning ground surveys); fence (comparable to a study that uses tagging to back-up a fence should it fail); and aggregate (carcasses recoverable by frequent surveys and those that would have flushed from the study area are available for analysis). The analysis is presented in four sections. First, I correct the data for sex and tag identification error, emigration from the study area, and immediate mortality. Second, I evaluate the data for sampling biases and handling stress. These analyses form the basis of recommendations for future study design changes, and the consideration of stratified population estimators. Third, I calculate population estimates using three estimators, the pooled Petersen (PPE), maximum likelihood Darroch (MLE) and Schaefer, and a variety of data stratification and pooling schemes. Fourth, I evaluate rules for choosing the most accurate of several stratified estimates and between that estimate and the PPE. Each rule is evaluated by comparing the mark-recapture estimates to the study area population estimate. These analyses exclude the estimates based solely on fence recoveries because, under normal field conditions, they would never be used in isolation to generate population estimates.

Data Corrections

Sex Identification Error: I correct sex identification error at application by comparing the sex of tagged fish recorded at release and recovery, and applying Staley's (1990) formula. Errors can result from the limited development of sexually dimorphic traits among newly arriving spawners (live fish cannot be examined internally) or simply from recording errors during the sometimes hectic tagging operation. It is unnecessary to correct the carcass recovery data because the carcasses were examined carefully and could be incised for internal examination.

Emigration from the Study Area: Emigrant sockeye are those that were tagged in the Stellako River and either spawned in the Nadina River or swam downstream past the fence. Because both populations were censused but neither was sampled for tag numbers, these fish are removed from the application total and their sex is estimated indirectly from the population sex ratio.

Tag Recognition Error: Resurvey data are used to correct the spawning ground recovery sample for tagged carcasses misidentified as being untagged on the initial survey. I estimate the number of missed tags as the product of the tag incidence in the resurvey and the number of carcasses examined in the initial survey.

Immediate Mortality and Handling Stress: Immediate mortality and other stress affects are evaluated in two steps: first, I examine the mark-recapture data for evidence of either stressed individuals or systemic stress; and second, I examine the additional data provided by the fence. Specific tags are excluded from the mark-recapture data if: a) chi-square tests show recovery rate is influenced by the need to ventilate the fish at release (all ventilated fish are excluded if the test result is significant); and b) a fish was recovered less than five days after release. The latter criterion is arbitrary; however, short times between application and recovery are typically associated with poor spawning success and likely reflect acute handling stress.

While not a data correction procedure, I additionally assess the data for evidence of stress, using chi-square tests to evaluate: a) spawning success among marked and unmarked female carcasses; and b) tag incidence and female spawning success among carcasses recovered near the fence (Area 9) versus further upstream. I interpret a significant test result as an indicator of stress sensitivity that may dictate future study design modifications. The fence also provides two additional types of data useful in the evaluation of stress: the daily migration into the study area, and the daily recovery of carcasses that would have flushed from the study area. I compare, for tagged and untagged sockeye, cumulative daily live immigration and carcass recoveries using a Kolmogorov-Smirnov two-sample test (Sokal and Rohlf 1981); a pattern of earlier recovery of tagged sockeye may be indicative of stress. I use carcasses recovered on the fence in: a) chi-square tests to evaluate differences between fence and spawning ground carcasses in numbers recovered within five days of release, tag incidence, and female spawning success; and b) a t-test to compare the elapsed time between tag-

ging and recovery. A significant difference in any test suggests stress may be a concern; a consistent difference among tests is interpreted as strong evidence that stress influences the recoverability of tagged fish.

Tests for Sampling Selectivity

The assumptions of equal probability of capture, simple random recovery sampling and complete mixing (Seber 1982, p 434-9) are assessed by testing the application and three recovery samples for: temporal, spatial, and sex biases using chi-square tests; and size bias using a Kolmogorov-Smirnov two-sample test. I assess application bias (unequal probability of capture and incomplete mixing) by stratifying the recovery sample (uncorrected for missed tags) and comparing the proportion tagged among strata. Recovery bias (nonrandom recovery sampling and incomplete mixing) is assessed by stratifying the application sample and comparing the proportions recovered.

Temporally, the application and recovery samples are stratified into five or six periods of approximately equal duration, sampling effort (recovery only; effort is not applicable to the capture method), and sample size. I interpret three significant results to be a true bias, while a single significant result may be a stratification artifact. Spatially, I aggregate recovery areas into three contiguous sections (plus the fence): lower (areas 7-9), middle (areas 4-6) and upper (areas 1-2) (Fig. 2). I examine size bias at recovery (application bias is not assessed because unmarked carcasses were not measured) by comparing the cumulative NF length-frequency distributions of recovered and non-recovered portions of the application sample.

Population Estimation

The study area population (excluding below-fence and Nadina spawners) is estimated from data adjusted for sex and tag recognition errors, emigration, and stress effects. I use the Stratified Population Analysis System (SPAS) software developed by Arnason *et al.* (1996) to calculate sex-specific population estimates for each recovery data set. The use of sex-specific data avoids potential biases resulting from differences in arrival timing and behaviour on the spawning grounds. The SPAS software calculates estimates and standard errors using the PPE (Seber 1982) and MLE (Plante 1990), as well as estimates (precision is not estimated) using the Schaefer estimator (Seber 1982). SPAS also performs two χ^2 tests that evaluate whether the mixing of tagged fish across recovery strata is independent of the application stratum (complete mixing), and whether mark proportions are equal across all recovery strata (equal proportions). These tests are identical to those described in the previous section but are specific to each stratification. Finally it provides the results of Plante's G^2 goodness-of-fit test for the MLE; nonsignificant ($p > 0.05$) results indicate acceptable model fit.

The MLE and Schaefer estimates are generated from *s:t* application:recovery matrices using temporal:temporal and temporal:spatial stratifications; spatial:spatial stratifications were uninformative because the single application stratum results in estimates equal to the PPE. Temporally, I stratify the data into 5-6 application and recovery periods with approximately equal numbers of tags applied or recovered. Spatially, I use 3-4 recovery strata, upper, middle and lower rivers and the fence, when appropriate. Pooling is often required to satisfy the assumptions of model fit, *i.e.*, to minimize the number of low recovery cells and reduce linear dependence in the recovery matrix. I also pool to evaluate model sensitivity and stability.

Schwarz and Taylor (1998; page 283) note that stratified Petersen models must satisfy the assumption that either: a) movement patterns, death and migration rates are the same for tagged and untagged fish in each stratum, in which case the population can only be estimated at time of tagging using a matrix constrained to $s \leq t$; or b) the population is closed with respect to movement among strata, in which case the population can only be estimated at time of recovery using a matrix constrained to $s \geq t$. Because the 1994 Stellako data more likely satisfy the latter; I use only $s \geq t$ matrices. Within that framework, I further pool the data as follows: a) only adjacent strata are pooled; b) strata with low or zero recovery cells are pooled first, followed by proportionally similar strata; and c) pooling continues until $s = t = 2$, at which point model fit is usually satisfied.

Estimator Selection

Schwarz and Taylor (1998) and Arnason *et al.* (1996) provide little practical advice regarding

decision rules for the selection of the most appropriate MLE or, indeed, for the rejection of a pooled Petersen in favour of a stratified estimate. Previous reports in this series (see Schubert 1998) use simple decision rules. The PPE is accepted when sampling biases are not detected. Otherwise, the MLE estimates are used. The PPE is rejected in favour of the MLE only when their confidence limits do not overlap.

Because the current study provides mark-recapture estimates for a study area population of known size, it permits an evaluation of estimation accuracy using alternate decision rules. I evaluate three options for choosing the most accurate MLE estimate; maximizing: the p-value of the G^2 test result; the size of the *s:t* matrix; and the product of the two. I also evaluate options for choosing the most accurate estimator among the PPE, MLE, or Schaefer, including maximizing the χ^2 and G^2 test p-value or precision, and considering other subjective information). Each option is evaluated by comparing the selected estimate with the study area escapement estimate.

RESULTS

VISUAL SURVEYS

The Stellako River above the fence was surveyed by boat on August 31, 1994; 7,250 sockeye were reported (Appendix 2). The river between the fence and the lagoon was surveyed four times from September 28 to October 12 (Appendix 2). To avoid counting sockeye migrating to the upper river, the surveys were delayed until spawning began in the area; consequently, the peak live count (5,000 sockeye) occurred on the first survey.

ENUMERATION FENCE

The fence operated from August 31 to October 12, 1994 (Appendix 3). Of the 122,672 live sockeye that arrived at the fence, 120,300 were permitted to swim upstream, 1,225 were tagged and released above the fence, 150 (100 females and 50 males) were killed for fecundity and parasite samples, and 997 males were harvested by native fishers. Four tagged fish migrated downstream past the counting box; sex and tag numbers were not observed. The peak daily count of 17,396 was on September 6, with the 50% migration on September 12; the migration was complete by mid-October. A total of 16,942 male, 12,897 female and 42 jack carcasses were recovered on the upstream side of the fence, of which 0.6%, 0.9% and 7.1%, respectively, had disk tags (Appendix 6). All were passed over the fence.

TAG APPLICATION

Disk tags were applied to 1,205 adults and 20 jacks from August 31 to October 1, 1994 (Appendix 3). Based on the total live count, 1.01% of the escapement was tagged, with the daily proportion ranging from 0.0% to 19.1%. This variability resulted from the sometimes conflicting demands of tagging and fence maintenance, and from unanticipated fluctuations in the migration. The mean NF length for males, females and jacks was 57.0, 55.3 cm and 47.3 cm, respectively; none were sampled for age. The incidence of net, lamprey and hook marks was 23%, 0% and 1% in males, 30%, 0% and 0% in females, and 15%, 0% and 0% in jacks, respectively (Appendix 4).

SPAWNING GROUND RECOVERY

Main Survey

The Stellako River was surveyed ten times (every 2-3 days) from September 26 to October 17, 1994, resulting in the recovery of 22,900 males, 29,705 females and 51 jacks (Appendix 5). Of the adults, 44% were male and 56% were female, of which 0.39% and 0.95% had disk tags. The most important recovery areas were areas 9 (29%) and 7, 4, 3, and 1 (11% each).

The average time between release and river recovery for disk tagged males, females and jacks was 21 days, 22 days and 21 days, respectively (Table 1). Time increased with distance travelled and decreased over the study. Tags were recovered on the fence in almost half the time of river recoveries. Spawning success averaged 94.5% and 78.7% among river and fence recoveries, respectively. Success was higher later in the recovery, especially among carcasses recovered on the fence (Table 1).

Resurvey

Previously surveyed areas of the Stellako River were resurveyed four times between October 4 and October 17, 1994 to recover 10,846 males,

Table 1. Average time between tag application and recovery and female spawning success (all recoveries), by recovery section, period and sex, in the Stellako River, 1994.

		Average days between tag application and carcass recovery [b]						Female spawning success	
Section [a]	Period [b]	Male	(n)	Female	(n)	Jack	(n)	%	(n)
Upper River	Early	26.5	(13)	29.1	(53)	24.0	(1)	90.0%	(2,487)
	Late	25.0	(1)	21.6	(27)	-	(0)	97.0%	(6,580)
	Total	26.4	(14)	26.6	(80)	24.0	(1)	95.1%	(9,067)
Middle River	Early	26.9	(13)	26.6	(39)	26.0	(1)	86.7%	(2,119)
	Late	18.2	(9)	19.1	(35)	22.0	(3)	97.3%	(4,923)
	Total	23.4	(22)	23.0	(74)	23.0	(4)	94.1%	(7,042)
Lower River	Early	23.3	(22)	23.8	(39)	23.0	(1)	91.6%	(7,752)
	Late	16.5	(31)	15.3	(89)	5.0	(1)	97.9%	(5,715)
	Total	19.3	(53)	17.9	(128)	14.0	(2)	94.3%	(13,467)
River Total	Early	25.1	(48)	26.8	(131)	23.5	(2)	90.4%	(12,358)
	Late	17.1	(41)	17.3	(151)	19.4	(5)	97.4%	(17,218)
	Total	21.4	(89)	21.6	(282)	20.6	(7)	94.5%	(29,576)
Fence Total	Early	18.6	(18)	17.1	(30)	16.0	(1)	64.4%	(6,482)
	Late	11.1	(88)	10.8	(96)	11.0	(2)	94.0%	(6,040)
	Total	12.3	(106)	12.3	(126)	12.7	(3)	78.7%	(12,522)

[a] Sections are: Upper River: areas 1,2, and 3; Middle River: areas 4, 5, and 6; Lower River: areas 7, 8, and 9.

[b] Time out to recovery: early = 31-Aug to 12-Sep releases; late = 13-Sep to 12-Oct releases. Female spawning success: early = 01-Sep to 03-Oct recoveries; late = 04-Oct to 17-Oct recoveries.

Table 2. Percent at age and mean POH length at age in Stellako River sockeye sampled on the spawning grounds, 1994.

		Percent at age				POH length (cm) at age			
Recovery location	Sample type	3/2	4/2	5/2	6/3	3/2	4/2	5/2	6/3
Stellako River	Male	0.0%	89.2%	10.8%	0.0%	-	45.7	49.2	-
	Female	0.0%	90.2%	9.8%	0.0%	-	45.2	49.7	-
	Jack	93.2%	6.8%	0.0%	0.0%	36.3	-	-	-

13,601 females and 14 jacks; 4, 26, and 0, respectively, had disk tags (Appendix 7).

BIOLOGICAL SAMPLING

The age composition of the adult carcass sample was 89% age 4_2 and 11% age 5_2 among males and 90% age 4_2 and 10% age 5_2 among females (Table 2; Appendix 9). No significant difference (t-test; $P > 0.05$) was noted in the age composition of males and females among the three sampling periods. Mean POH length at age is provided in Table 2; mean POH and standard lengths are provided in Appendix 9. The jack sample was 93% age 3_2 and 7% age 4_2; therefore, the 50 cm NF cut-off to separate jacks and adults introduced some error into the estimates.

ESCAPEMENT ESTIMATE

Stellako River

There are three components of the 1994 Stellako River sockeye escapement estimate. The first is the escapement of Stellako spawners that entered the river before the fence was closed. Based on the August 31 observation of 7,250 sockeye holding in the river (no carcasses had

Table 3. Stellako River sockeye salmon escapement estimates, by age and sex, estimated from fence counts and visual observations, 1994.

Sex	Above fence estimate: Not enumerated at fence [a,b]	Above fence estimate: Enumerated at fence [b,c]	Below fence estimate	Total Stellako River escapement [d]	Escapement at age: 3_2	Escapement at age: 4_2	Escapement at age: 5_2
Male	6,297	58,546	1,652	66,495	0	59,295	7,200
Female	6,735	62,608	2,144	71,487	0	64,503	6,984
Total	13,032	121,154	3,796	137,982	0	123,798	14,184
Jack	18	173	5	196	183	13	0

[a] Stellako River spawners which entered the river before the fence was installed.

[b] Jack and sex-specific adult escapements were estimated from the total carcass recovery sample.

[c] Estimate excludes 99 males and 99 females which were counted at the fence but spawned in the Nadina Channel; jack and sex-specific adult escapements to Nadina were estimated from spawning channel carcass recoveries.

[d] Excludes 1,047 males and 100 females which were killed for fecundity samples or harvested by native fishers.

been recovered), I estimate this population at 13,050 sockeye (Table 3), 9% of the total. Second, 121,525 sockeye of either Nadina or Stellako origin were counted at the fence from August 31 until the run was complete. I estimate the Nadina component of this total at 99 males and 99 females, based on a recovery of two disk tagged sockeye (one of each sex) in the Nadina Spawning Channel (C. Harrison, pers. comm.) and a mean tag incidence at the fence of 1.01% (Appendix 3). The Stellako component, the difference between the fence count and the Nadina estimate, is 121,327 sockeye (Table 3), 88% of the total. Third, the below-fence population is estimated from two data sources: the daily visual counts below the fence (Appendix 2) minus the fence counts on the two subsequent days; and a mean spawner residence time of 10.6 days, as estimated from sockeye tagged on or after September 28 and recovered on the spawning grounds. I estimate this population at 3,801 sockeye (Table 3), 3% of the total. The sum of these three components produces a total Stellako River escapement of 138,178 sockeye.

The escapement is partitioned among males, females and jacks based on their respective proportions in the total carcass recovery sample (Table 4). These recoveries comprise over 60% of the estimated population and, because the fence creates a closed system for carcasses, include all but those that rotted in deep water or were removed by predators. I estimate the escapement, corrected for the assignment of small adult males to the jack group, at 66,508 adult males, 71,487 females, and 183 jacks. The escapement by sex and age is reported in Table 3.

Study Area

The study area escapement, uncorrected for jack identification error to maintain consistency with the mark-recapture estimate, is estimated at 64,843 males, 69,343 females, and 191 jacks (Table 3).

MARK-RECAPTURE STUDY

Data Corrections

The raw mark-recapture data (appendices 3, 5, 6 and 7), adjusted for sex identification error, emigration from the study area, tag recognition error and handling stress, are presented in Table 4. The adjustments are described below.

Sex Identification Error: The sex of 5 (2.6%) males and 11 (2.7%) females was recorded incorrectly at the time of tagging. When adjusted for this error, 328 (27.2%) males and 877 (72.8%) females were released with disk tags (Appendix 3).

Emigration from the Study Area: I adjusted the application total for tagged fish observed emigrating from the study area or spawning in other areas (individual tags were not removed because tag numbers were not recorded). This includes:

Table 4. Disk tags applied at the enumeration fence, and carcasses examined and disk tags recovered at the fence and on the spawning grounds, by sex, for Stellako River sockeye salmon, 1994.

Mark-recapture analysis	Sex	Tags and marks applied [a]	Carcasses examined	Tags recovered			% recovered	Tag incidence
				Tag only	Resurvey adjustment	Total		
Spawning grounds	Male	325	22,900	89	8	97	30.0%	0.4%
	Female	873 [b]	29,705 [b]	282 [b]	57	339 [b]	38.8%	1.1%
	Jack	20	51	7	0	7	35.0%	13.7%
Enumeration fence	Male	320 [c]	16,942 [c]	101 [c]	0	101 [c]	31.6%	0.6%
	Female	864 [c]	12,897 [c]	116 [c]	0	116 [c]	13.4%	0.9%
	Jack	20	42	3	0	3	15.0%	7.1%
Total	Male	320	39,842	190	8	198	62.0%	0.5%
	Female	863	42,602	398	57	455	52.7%	1.1%
	Jack	20	93	10	0	10	50.0%	10.8%

[a] Corrected for sex identification errors; secondary marks were not applied in 1994. Totals exclude 1 male and 1 female disk tagged sockeye which emigrated to the Nadina River, and 2 male and 2 female disk tagged sockeye which emigrated past the fence.

[b] Excludes 1 female disk tagged sockeye which was recovered on the spawning grounds less than 5-days after release.

[c] Excludes 5 male and 10 female disk tagged sockeye which were recovered on the fence less than 5-days after release.

two Nadina sockeye that were tagged at the fence and migrated to the Nadina River (sex is estimated from the spawning channel carcass census (1:1) (C. Harrison, pers. comm.)); and four tagged Stellako sockeye that migrated downstream past the fence when the counting box was in operation (sex is estimated from the tagged carcasses recovered at the fence (1:1)) (Table 4). Nithi sockeye, a stock that spawns upstream from the Stellako River, are not considered because their escapement was negligible (Schubert 1998).

Handling Stress: In a standard mark-recapture study, salmon are captured in the river using nets, tagged, and recovered as carcasses. The data generated from such studies permit a two-step evaluation of stress. First, specific fish are removed from the application sample if their recovery pattern is indicative of stress at release. I removed tagged sockeye that had been recovered less than five days after release: one female recovered on the spawning grounds, and five males and ten females recovered at the fence. I also partitioned the application sample into fish that required ventilation at release and those that did not: 12 males (3.7%) and 26 females (3.0%) required ventilation. The proportions recovered on either the spawning grounds or the fence (16.7% of the males and 30.8% of the females) were not significantly different ($P > 0.05$; chi-square) from the nonventilated fish (27.5% and 32.2%); consequently, I did not remove them from the sample. Second, two tests serve as general indicators of stress: a) spawning success is compared between tagged and untagged females; and b) tag incidences and spawning success are compared between fish recovered near the tagging site (Area 9) and further upstream (areas 1-8). There is no significant difference ($P > 0.05$; chi-square) in: spawning success between tagged (91.6%) and untagged (94.4%) females, as indicated by the proportion of incomplete spawners (0% and 50% spawned); disk tag incidence between carcasses recovered near the tagging site (0.5% and 0.9% in males and females, respectively) and further upstream (0.4% and 1.0%); or in female spawning success among all carcasses recovered in the lower river (94.3%) and the middle (94.1%) and upper (95.1%) river. None of these results indicate stress biased the population estimates.

The fence provides two daily counts that are unavailable to standard mark-recapture studies: untagged fish into the study area; and carcasses that would have flushed from the study area. I compare the cumulative frequency distributions of tagged vs. untagged fish at release and recovery in Fig. 3. In general, tagged fish were released

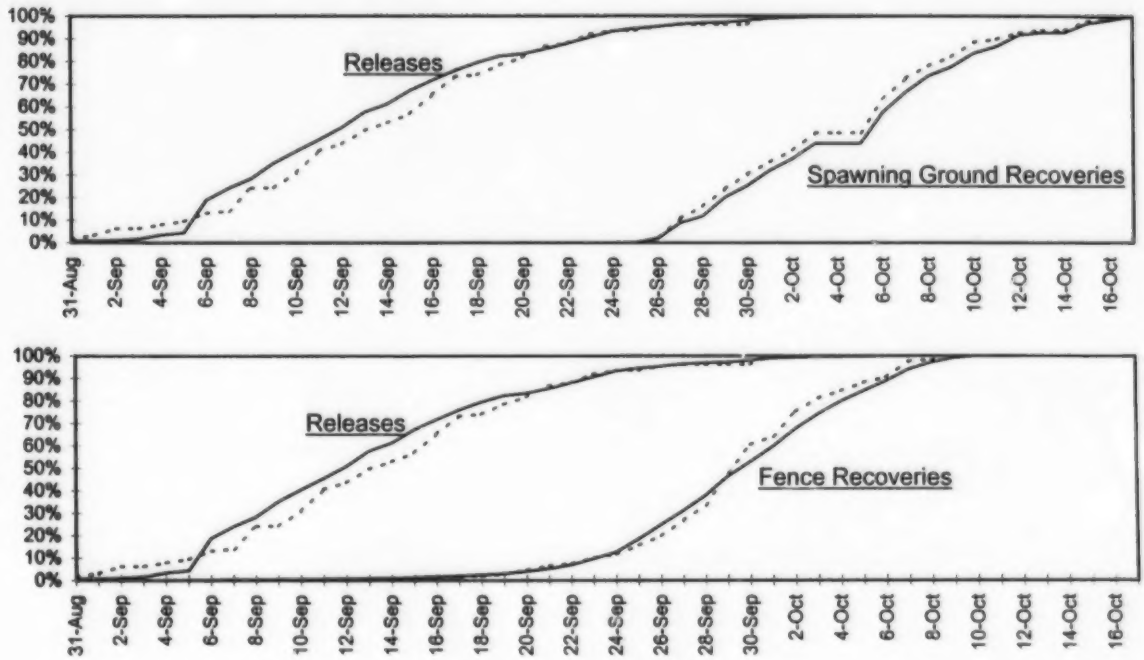

Figure 3. Daily percent cumulative release of disk tagged (dashed lines) and untagged (solid lines) sockeye at the Stellako River enumeration fence, and daily percent cumulative recovery of disk tagged (dashed lines) and untagged (solid lines) sockeye carcasses on the spawning grounds and at the enumeration fence.

later but recovered earlier than untagged fish, i.e. their post-release lifespan was shorter. Among the spawning ground recoveries, this pattern was consistent but not significant ($P > 0.05$, Kolmogorov-Smirnov two-sample test); among the fence recoveries, the difference was significant ($P < 0.05$) but the pattern of earlier recovery of tagged fish did not became apparent until later in the study. The comparison of river and fence recoveries (Table 5) shows: a) a shorter elapsed time for tagged fish recovered on the fence (12 days) vs. the spawning grounds (21 days), and a higher proportion that was recovered within five days (6.5% vs. 0.2%); b) a higher tag incidence at the fence among males (0.63% vs. 0.39%) and females (0.98% vs. 0.95%), although the difference was significant only among males; and c) spawning success of fence recoveries was lower than river recoveries, both in total (78.7% vs. 94.5%) and among tagged fish (65.9% vs. 91.7%). These observations, that tagged fish may have a shorter post-release life span and a greater tendency to flush out of the system and in an unspawned condition than untagged fish, all suggest that stress may have biased the population estimates.

Tag Recognition Error: Based on the resurvey data, I estimated that 8 (8.2%), 57 (16.8%) and 0 (0.0%) tagged males, females and jacks, respectively, had been incorrectly identified as tagged fish on the initial survey (Table 4). When corrected for this error, 97 male, 339 female and 7 jack disk tags were recovered, a tag incidence of 0.4%, 1.1% and 13.7%, respectively.

Sampling Selectivity

I evaluate sampling selectivity in the application and recovery samples for each of the spawning ground, fence, and aggregate carcass recovery groups. The results are presented below and summarized in Table 6. The actual data and test results are detailed in appendices 10-15.

Spawning Ground: I did not detect a significant temporal bias in the application sample (Ta-

Table 5. Comparison of elapsed time from release to recovery, female spawning success, disk tag incidence, recovery rate, sex at recovery, and mean size of disk tagged carcasses, between spawning ground and enumeration fence recoveries of sockeye carcasses in the Stellako River, 1994.

		Males			Females		
Comparison of	Test	River recovery	Fence recovery	Test result [a]	River recovery	Fence recovery	Test result [a]
Mean time from release to recovery (days)	t-test	21.4	12.3	sd	21.6	12.3	sd
Tags recovered within 5-days	-	0	5	-	1	10	-
Percent	Chi-square	0.0%	4.7%	ns	0.3%	7.9%	hsd
Spawning success (%)	Chi-square	-	-	-	94.5%	78.7%	sd
Disk tag incidence (%)	Chi-square	0.39%	0.63%	sd	0.95%	0.98%	ns
Tag recovery rate [b]	Chi-square	30.0%	45.4%	hsd	38.8%	22.1%	hsd
Sex at recovery (%)	Chi-square	43.5%	56.8%	hsd	56.5%	43.2%	hsd
Mean size of disk tagged carcasses (cm)	t-test	57.2	57.0	ns	55.2	55.1	ns

[a] Definitions: ns - not significant; sd - significant difference ($P < 0.05$); hsd - highly significant difference ($P < 0.005$).

[b] From Table 4. Excludes tags recovered less than 5-days after release on the spawning grounds. Recovery rate at the fence calculated as tags recovered at the fence divided by the number released minus those recovered on the spawning grounds.

Table 6. Sample bias profile by sample type for the 1994 Stellako River sockeye salmon escapement estimation study. Recovery data are stratified by spawning ground, enumeration fence, and aggregate recoveries.

			Spawning ground recoveries		Enumeration fence recoveries		Aggregate recoveries	
Bias type	Test of	Among	Test result	Observation	Test result	Observation	Test result	Observation
			Application Sample					
Temporal	Tag incidence	Equal recovery periods	ns	Both sexes	sd	Both sexes	hsd	Males
		Equal recovery effort	ns	Both sexes	-	-	hsd	Males
		Equal numbers of recoveries	ns	Both sexes	sd	Females	hsd	Males
				↓ late		↓ early		↓ late
Spatial	Tag incidence	River (3) and fence	ns	Males	hsd	Males	hsd	Males
				↑ lower river		↑ at fence		↑ at fence
Fish sex	Sex ratio	Marked/unmarked recoveries	hsd	↑ female tag	sd	↑ female tag	hsd	↑ female tag
			Recovery Sample					
Temporal	Recovery rate	Equal application periods	hsd	Both sexes	hsd	Both sexes	sd	Both sexes
		Equal numbers applied	hsd	Both sexes	hsd	Both sexes	sd	Both sexes
				↓ late		↑ late		↑ late
Fish size	Size-freq. dist.	Recovered/nonrecovered tags	ns	Both sexes	ns	Both sexes	ns	Both sexes
Fish sex	Sex ratio	Recovered/nonrecovered tags	sd	↑ female recov	hsd	↓ female recov	sd	↓ female recov

ble 6), although tag incidences in both sexes decline with time (Appendix 10a). In contrast, the tag recovery rate differs significantly among application periods. In both sexes, recovery rates among the first three or four application periods are similar (28% to 36%), and much higher than in the final period (9% to 18%) (Appendix 11a). This combination of lower recovery rates and (perhaps) tag incidences in the same period can introduce a negative bias in the population estimates.

I also failed to detect a significant spatial bias among carcasses recovered in the river (Table 6). Female tag incidences are similar at 0.9% to 1.1% (Appendix 12), while in males there is a lower tag incidence (0.23%) in the upper river (among fish tagged early in the study period (Appendix 13)) that approaches significance. The middle (0.41%) and lower (0.46%) river tag incidences are almost double that of the upper river. Because the upper river spawners would be available for recovery as carcasses in a larger part of the study area, their recovery rate may also be higher (this cannot be confirmed because only one tag site was used). If so, their lower tag incidence would introduce a positive bias in the population estimate.

The size distributions of recovered and unrecovered tagged fish is not significantly different in either sex (Appendix 14). The river surveys, therefore, were not selective by size.

Sex bias is evident at both application and recovery (Table 6). The male:female ratios among tagged (0.3:1) and untagged (0.8:1) recoveries (Appendix 15) show the application sample is selective for females despite attempts to tag in proportion to daily abundance. Similarly, the ratios among recovered (0.3:1) and unrecovered (0.4:1) tagged fish show the recovery sample is also selective for females. Because I calculate sex-specific population estimates, this type of selectivity will not bias the population estimates.

Enumeration Fence: There is a significant temporal bias in the application sample (Table 6). Tag incidences are lower late (and perhaps early) in the die-off in both females (significant in both stratifications) and males (one stratification) (Appendix 10b). There is also a significant temporal bias in tag recovery rates, with higher rates later in the run (Table 6). Male recovery rates increase from 5%-7% in the first period to 36%-58% in the final three periods (Appendix 11b). Female recovery rates increase from 4% to 11%-45%. The combination of lower tag incidences and higher recovery rates in the same period can introduce a positive bias in the population estimates.

Among females, there is no difference in the tag incidence of river and fence carcass recoveries (Table 6; Appendix 12). Among males, however, the tag incidence at the fence (0.60%) is significantly different than in the river (0.39%).

The size distributions of recovered and unrecovered tagged fish is not significantly different in either sex (Appendix 14). The fence, therefore, did not recover carcasses in a size selective manner.

Sex bias is evident at both application and recovery (Table 6). The male:female ratios among tagged (0.9:1) and untagged (1.3:1) recoveries (Appendix 15) show the application sample is selective for females. In contrast, the ratios among recovered (0.9:1) and unrecovered (0.3:1) tagged fish shows that the recovery sample is selective for males, a bias opposite to that reported on the spawning grounds. Because I calculate sex-specific population estimates, this type of selectivity will not bias the population estimates.

Aggregate: Among females, tag incidences in the combined spawning ground and fence samples are temporally similar, ranging from 0.7% to 1.2% (Table 6; Appendix 10c). In males, however, there are highly significant temporal differences, with lower incidences late in the die-off. The tag recovery rates are also significantly different among application periods, with much lower recovery rates in the early periods (Appendix 11c). Recovery rates increase from 39%-43% in the first period to 63%-73% in the final three periods. Because the application and recovery biases among males are in opposite directions, however, the population estimate may be largely unbiased.

The spatial and size distributions described for the spawning grounds and fence also apply to the aggregate sample (Table 6). The female tag incidence is similar among river and fence recoveries, while the male tag incidence declines with distance above the fence (Appendix 12). The size distributions of recovered and unrecovered tagged fish is not significantly different in either sex (Appendix 14).

Table 7a. Temporally:temporally stratified application:recovery matrices used for the mark-recapture population estimates of Stellako River sockeye, 1994.

Application period	Tags applied	Spawning ground recovery period 1) 26-Sep to 29-Sep	2) 30-Sep to 02-Oct	3) 03-Oct to 06-Oct	4) 07-Oct to 09-Oct	5) 10-Oct to 17-Oct	Percent recovered
Spawning Ground Recoveries, Males							
1) 31-Aug to 08-Sep	90	14.2	7.6	6.5	5.4	1.1	38.8%
2) 09-Sep to 12-Sep	49	4.4	4.4	4.4	2.2	2.2	35.6%
3) 13-Sep to 16-Sep	60	5.4	5.4	3.3	4.4	2.2	34.5%
4) 17-Sep to 20-Sep	53	3.3	3.3	3.3	3.3	3.3	30.8%
5) 21-Sep to 01-Oct	73	1.1	0.0	0.0	5.4	1.1	10.5%
Total tags	325	28.3	20.7	17.4	20.7	9.8	-
Total recovery	-	4,870	4,196	4,867	4,449	4,518	-
Percent tagged	-	0.58%	0.49%	0.36%	0.47%	0.22%	-
Spawning Ground Recoveries, Females							
1) 31-Aug to 08-Sep	200	14.4	18.0	16.8	10.8	16.8	38.5%
2) 09-Sep to 12-Sep	183	18.0	7.2	24.0	10.8	20.4	44.0%
3) 13-Sep to 16-Sep	198	27.6	14.4	18.0	16.8	10.8	44.3%
4) 17-Sep to 20-Sep	145	10.8	8.4	14.4	16.8	12.0	43.1%
5) 21-Sep to 01-Oct	147	3.6	4.8	8.4	4.8	9.6	21.3%
Total tags	873	74.5	52.9	81.7	60.1	69.7	-
Total recovery	-	5,671	4,791	5,961	6,003	7,279	-
Percent tagged	-	1.31%	1.10%	1.37%	1.00%	0.96%	-

Application period	Tags applied	Enumeration fence recovery period 1) 01-Sep to 27-Sep	2) 28-Sep to 30-Sep	3) 01-Oct to 03-Oct	4) 04-Oct to 06-Oct	5) 07-Oct to 12-Oct	Percent recovered
Enumeration Fence Recoveries, Males							
1) 31-Aug to 08-Sep	88	0	2	2	2	0	6.8%
2) 09-Sep to 12-Sep	49	5	2	3	0	0	20.4%
3) 13-Sep to 16-Sep	60	7	7	5	1	2	36.7%
4) 17-Sep to 20-Sep	52	5	7	3	6	0	40.4%
5) 21-Sep to 01-Oct	71	0	7	19	7	9	59.2%
Total tags	320	17	25	32	16	11	-
Total recovery	-	2,[illegible]7	4,008	4,211	3,279	2,637	-
Percent tagged	-	0.61%	0.62%	0.76%	0.49%	0.42%	-
Enumeration Fence Recoveries, Female							
1) 31-Aug to 08-Sep	198	4	1	2	0	1	4.0%
2) 09-Sep to 12-Sep	182	6	6	1	5	1	10.4%
3) 13-Sep to 16-Sep	197	4	3	9	3	2	10.7%
4) 17-Sep to 20-Sep	143	3	2	6	2	2	10.5%
5) 21-Sep to 01-Oct	144	0	2	16	18	17	36.8%
Total tags	864	17	14	34	28	23	-
Total recovery	-	2,739	1,786	2,272	2,724	3,376	-
Percent tagged	-	0.62%	0.78%	1.50%	1.03%	0.68%	-

Continued

Table 7a. Temporally:temporally stratified application:recovery matrices used for the mark-recapture population estimates of Stellako River sockeye, 1994, continued.

Application period	Tags applied	Combined recovery period 1) 01-Sep to 28-Sep	2) 29-Sep to 01-Oct	3) 02-Oct to 04-Oct	4) 05-Oct to 06-Oct	5) 07-Oct to 09-Oct	6) 10-Oct to 17-Oct	Percent recovered
Combined spawning ground and fence recoveries, male								
1) 31-Aug to 08-Sep	88	10.8	12.8	4.3	6.4	5.4	1.1	46.5%
2) 09-Sep to 12-Sep	49	9.3	7.4	4.2	2.2	2.2	2.2	56.0%
3) 13-Sep to 16-Sep	60	12.4	13.4	6.2	2.2	6.4	2.2	71.2%
4) 17-Sep to 20-Sep	52	6.1	13.4	9.3	2.1	3.3	3.3	71.8%
5) 21-Sep to 01-Oct	71	2.0	13.1	17.0	2.0	13.4	2.1	69.9%
Total tags	320	40.5	60.2	40.9	14.9	30.7	10.8	-
Total recovery	-	6,820	9,483	6,881	5,054	6,378	5,226	-
Percent tagged	-	0.59%	0.63%	0.59%	0.29%	0.48%	0.21%	-
Combined spawning ground and fence recoveries, female								
1) 31-Aug to 08-Sep	198	14.8	14.2	12.8	14.4	11.8	16.8	42.9%
2) 09-Sep to 12-Sep	182	22.4	14.6	11.8	18.4	11.8	20.4	54.7%
3) 13-Sep to 16-Sep	197	19.4	30.8	13.2	15.6	17.8	11.8	55.2%
4) 17-Sep to 20-Sep	143	12.4	14.6	10.2	9.4	18.8	12.0	54.2%
5) 21-Sep to 01-Oct	143	2.4	11.6	26.6	12.2	18.8	12.6	58.9%
Total tags	863	71.5	85.9	74.7	70.1	79.1	73.7	-
Total recovery	-	6,816	7,538	5,770	5,820	8,323	8,335	-
Percent tagged	-	1.05%	1.14%	1.29%	1.20%	0.95%	0.88%	-

Sex bias is evident at both application and recovery (Table 6). The male:female ratios among tagged (0.4:1) and untagged (0.9:1) recoveries (Appendix 15) show the application sample is selective for females. In contrast, the ratios among recovered (0.4:1) and unrecovered (0.3:1) tagged fish show the recovery sample is selective for males. This bias is similar to the river survey but opposite the fence recoveries. The same pattern is evident in the recovery rates of tagged males and females in the river (30.0% and 38.8%) and at the fence (31.6% and 13.4%) (Table 4).

Population Estimates

I present the sex-specific population estimates, calculated using the pooled Petersen (PPE), maximum likelihood Darroch (MLE) and Schaefer estimators, plus the SPAS "complete mixing" and "equal proportions" (χ^2) and Plante's "goodness of fit" (G^2) test results, and comparisons with the known study area escapement (64,843 males and 69,343 females; p. 11), in Table 8. The PPE estimates are calculated from the fully pooled data in Table 4; MLE and Schaefer estimates are calculated from the initial stratifications (and subsequent pooling) presented in Table 7.

Spawning Ground Recoveries: The male and female PPE estimates and 95% confidence intervals (CI) calculated from spawning ground recoveries are 76,172 ± 12,521 (±16%) and 76,359 ± 6,299 (±8%), respectively (Table 8a). Relative to the known study area population, these estimates have a positive bias of 18% and 10%, respectively. The confidence interval of the male PPE estimate includes the known study area population, while that of the female PPE estimate does not.

The Schaefer estimates are robust to pooling but do not substantially improve on the accuracy of the PPE. The male and female estimates range from 74,406 to 79,075 and 76,407 to 76,687, respectively, with positive biases ranging from 15% to 22% among males and 10% to 11% among females.

The MLE failed to produce an estimate in over one-half of the 38 pooling scenarios (Table 8a). Such failures can be caused by zero or near

Table 7b. Temporally:spatially stratified application:recovery matrices used for the mark-recapture population estimates of Stellako River sockeye, 1994.

Application period	Tags applied	Recovery location: 1) Upper river	2) Middle river	3) Lower river	Percent recovered
		Spawning Ground Recoveries, Males			
1) 31-Aug to 08-Sep	90	10.9	10.9	13.1	38.8%
2) 09-Sep to 12-Sep	49	3.3	3.3	10.9	35.6%
3) 13-Sep to 16-Sep	60	1.1	5.4	14.2	34.5%
4) 17-Sep to 20-Sep	53	0.0	3.3	13.1	30.8%
5) 21-Sep to 01-Oct	73	0.0	1.1	6.5	10.5%
Total tags	325	15.3	24.0	57.8	-
Total recovery	-	6,102	5,367	11,431	-
Percent tagged	-	0.25%	0.45%	0.51%	-
		Spawning Ground Recoveries, Females			
1) 31-Aug to 08-Sep	200	39.7	19.2	18.0	38.5%
2) 09-Sep to 12-Sep	183	24.0	27.6	28.9	44.0%
3) 13-Sep to 16-Sep	198	19.2	15.6	52.9	44.3%
4) 17-Sep to 20-Sep	145	10.8	19.2	32.5	43.1%
5) 21-Sep to 01-Oct	147	2.4	7.2	21.6	21.3%
Total tags	873	96.2	89.0	153.9	-
Total recovery	-	9,068	7,069	13,568	-
Percent tagged	-	1.06%	1.26%	1.13%	-

Application period	Tags applied	Recovery location: 1) Upper river	2) Middle river	3) Lower river	4) Fence	Percent recovered
		Combined Recoveries, Males				
1) 31-Aug to 08-Sep	88	10.9	10.9	13.1	6.0	46.5%
2) 09-Sep to 12-Sep	49	3.3	3.3	10.9	10.0	56.0%
3) 13-Sep to 16-Sep	60	1.1	5.4	14.2	22.0	71.2%
4) 17-Sep to 20-Sep	52	0.0	3.3	13.1	21.0	71.8%
5) 21-Sep to 01-Oct	71	0.0	1.1	6.5	42.0	69.9%
Total tags	320	15	24	58	101	-
Total recovery	-	6,102	5,367	11,431	16,942	-
Percent tagged	-	0.25%	0.45%	0.51%	0.60%	-
		Combined Recoveries, Female				
1) 31-Aug to 08-Sep	198	39.7	19.2	18.0	8.0	42.9%
2) 09-Sep to 12-Sep	182	24.0	27.6	28.9	19.0	54.7%
3) 13-Sep to 16-Sep	197	19.2	15.6	52.9	21.0	55.2%
4) 17-Sep to 20-Sep	143	10.8	19.2	32.5	15.0	54.2%
5) 21-Sep to 01-Oct	143	2.4	7.2	21.6	53.0	58.9%
Total tags	863	96	89	154	116	-
Total recovery	-	9,068	7,069	13,568	12,897	-
Percent tagged	-	1.06%	1.26%	1.13%	0.90%	-

zero recovery cells or near linear dependencies (Schwarz and Taylor 1998). Among the six male stratifications that produce estimates, the SPAS complete mixing, equal proportions, and Plante's G^2 test results exceed 0.05 in 0, 5, and 2 cases, respectively. The population estimates are neither robust to pooling nor particularly precise: they are distributed over an almost two-fold range, from 63,409 to 102,246; and their 95% CI's range from ±19% to ±42%. The temporal:spatial stratifications produce more accurate estimates than the PPE; the temporal:temporal estimates increase the error to as high as +58%. The 95% CI's of all of the estimates include the known study area population; however, this in some cases reflects low precision rather than accuracy. Among the 12 female stratifications that produce estimates, the SPAS complete mixing, equal proportions, and Plante's G^2 test results exceed 0.05 in 4, 12, and 2 cases, respectively. The female estimates are both robust to pooling and precise (95% CI's similar to the PPE): the estimates range from 74,463 to 81,176; and the 95% CI's range from ±9% to ±17%. Four of the stratifications produce estimates that improve on the accuracy of the PPE by at least 1%, eight produce estimates that are within 1%, and one increases the error (to 17%). Overall, the MLE estimates the population with a positive bias ranging from 7% to 17%; with only four exceptions, the 95% CI's do not include the known study area population.

Enumeration Fence Recoveries: The male and female PPE estimates and 95% CI's calculated from enumeration fence recoveries are 53,320 ± 8,480 (±16%) and 95,356 ± 20,927 (±22%), respectively (Table 8b). Relative to the known study area population, these estimates are highly biased, with errors of -18% and +38%, respectively. Neither of the 95% CI's include the known study area population.

The Schaefer estimates are robust to pooling; the estimator does not substantially improve the accuracy of the male estimates and increase the error of the female estimates. The estimates range from 52,801 to 53,581 for males and 99,873 to 102,096, for females; biases range from -17% to -19% among males and +44% to +47% among females.

The MLE failed to produce an estimate in 13 of the 20 pooling scenarios (Table 8b) due to zero or near zero recovery cells or near linear dependencies. Among the three male stratifications that produce estimates, the SPAS complete mixing, equal proportions, and Plante's G^2 test results exceed 0.05 in 0, 3, and 0 cases, respectively. These estimates are robust to pooling but relatively imprecise: the estimates range from 52,312 to 53,271; and the 95% CI's range from ±19% to ±25%. The MLE produced estimates with errors (-18% to -19%) of the same magnitude as the PPE; the 95% CI's of only one of the estimates include the known study area population. Among the four female stratifications that produce estimates, the SPAS complete mixing, equal proportions, and Plante's G^2 test results exceed 0.05 in 0, 3, and 3 cases, respectively. The female estimates are also robust to pooling but imprecise: the estimates range from 118,184 to 118,381; and the 95% CI's are all ±30%. The MLE produces estimates that almost double (to 70%-71%) the already large error of the PPE (38%); none of the 95% CI's include the known study area population.

Aggregate Recoveries: The male and female PPE estimates and 95% CI's calculated from the aggregate recoveries are 64,265 ± 5,477 (±9%) (Table 8c) and 80,717 ± 5,058 (±6%) (Table 8d), respectively. Relative to the known study area population, the male estimate is almost unbiased (-1%) while the female estimate has an error of +16%. The CI of the male estimate includes the known study area population, while that of the female estimate does not.

The Schaefer estimator produces estimates that are robust to pooling, but do not substantially improve on the accuracy of the PPE. The male and female estimates range from 64,109 to 66,115 and 80,539 to 80,836, respectively, with biases ranging from -1% to +2% among males and +16% to +17% among females.

The MLE failed to produce an estimate in one-half of the 58 pooling scenarios (Table 8c, 8d) due to zero or near zero recovery cells or near linear dependencies. Among the 12 male stratifications that produce estimates, the SPAS complete mixing, equal proportions, and Plante's G^2 test results exceed 0.05 in 0, 03, and 7 cases, respectively. These estimates are somewhat robust to pooling and relatively precise: the estimates range from 57,214 to 74,105; and the 95% CI's range

Table 8a. Escapement estimates for 1994 Stellako River sockeye males and females calculated using Petersen, Darroch, and Schaefer estimators under various stratification and pooling scenarios: *spawning ground recovery data only.*

		Petersen estimator			ML Darroch estimator			Schaefer estimator		SPAS Test Results		
Sex	Pooling [a]	Estimate	+/- 95% cl	% Dev [b]	Estimate	+/- 95% cl	% Dev [b]	Estimate	% Dev [b]	*Complete mixing*	*Equal propns*	*Plante's* G^2
Male	P: 1x1	76,172	12,521	17.5%	-	-	-	-	-	-	-	-
	T: 5x5	-	-	-	[c]	-	-	77,501	19.5%	*0.00*	*0.07*	-
	T: 5x4	-	-	-	[c]	-	-	78,999	21.8%	*0.00*	*0.15*	-
	T: 5x3	-	-	-	[c]	-	-	79,075	21.9%	*0.00*	*0.09*	-
	T: 5x2	-	-	-	[c]	-	-	78,829	21.6%	*0.00*	*0.03*	-
	T: 4x4	-	-	-	[c]	-	-	78,072	20.4%	*0.01*	*0.15*	-
	T: 4x3	-	-	-	90,973	40,393	40.3%	78,055	20.4%	*0.01*	*0.09*	*0.09*
	T: 4x2	-	-	-	[c]	-	-	77,953	20.2%	*0.01*	*0.03*	-
	T: 3x3	-	-	-	[c]	-	-	78,057	20.4%	*0.00*	*0.09*	-
	T: 3x2	-	-	-	[c]	-	-	77,955	20.2%	*0.00*	*0.03*	-
	T: 2x2	-	-	-	102,246	43,080	57.7%	77,897	20.1%	*0.00*	*0.03*	-
	TS: 5x3	-	-	-	[c]	-	-	74,406	14.7%	*0.00*	*0.04*	-
	TS: 5x2	-	-	-	64,949	13,343	0.2%	75,127	15.9%	*0.00*	*0.06*	*0.00*
	TS: 4x3	-	-	-	[c]	-	-	74,445	14.8%	*0.00*	*0.04*	-
	TS: 4x2	-	-	-	63,409	12,355	-2.2%	75,162	15.9%	*0.00*	*0.06*	*0.00*
	TS: 3x3	-	-	-	[c]	-	-	74,789	15.3%	*0.03*	*0.04*	-
	TS: 3x2	-	-	-	68,343	15,017	5.4%	75,636	16.6%	*0.03*	*0.06*	*0.34*
	TS: 2x2	-	-	-	65,567	17,950	1.1%	75,699	16.7%	*0.01*	*0.06*	-
Female	P: 1x1	76,359	6,299	10.1%	-	-	-	-	-	-	-	-
	T: 5x5	-	-	-	[c]	-	-	76,687	10.6%	*0.00*	*0.11*	-
	T: 5x4	-	-	-	[c]	-	-	76,618	10.5%	*0.00*	*0.09*	-
	T: 5x3	-	-	-	[c]	-	-	76,595	10.5%	*0.00*	*0.04*	-
	T: 5x2	-	-	-	74,463	6,971	7.4%	76,559	10.4%	*0.00*	*0.36*	*0.00*
	T: 4x4	-	-	-	[c]	-	-	76,610	10.5%	*0.02*	*0.09*	-
	T: 4x3	-	-	-	[c]	-	-	76,613	10.5%	*0.02*	*0.04*	-
	T: 4x2	-	-	-	[c]	-	-	76,542	10.4%	*0.02*	*0.36*	-
	T: 3x3	-	-	-	[c]	-	-	76,612	10.5%	*0.01*	*0.04*	-
	T: 3x2	-	-	-	[c]	-	-	76,541	10.4%	*0.01*	*0.36*	-
	T: 2x2	-	-	-	81,176	13,589	17.1%	76,545	10.4%	*0.00*	*0.36*	-
	TS: 5x3	-	-	-	76,952	7,438	11.0%	76,461	10.3%	*0.00*	*0.50*	*0.00*
	TS: 5x2	-	-	-	76,641	6,798	10.5%	76,514	10.3%	*0.00*	*0.92*	*0.00*
	TS: 5x2*	-	-	-	75,486	6,567	8.9%	76,407	10.2%	*0.00*	*0.39*	*0.00*
	TS: 4x3	-	-	-	75,028	7,149	8.2%	76,457	10.3%	*0.02*	*0.50*	*0.01*
	TS: 4x2	-	-	-	76,553	6,424	10.4%	76,505	10.3%	*0.02*	*0.92*	*0.01*
	TS: 4x2*	-	-	-	76,000	6,414	9.6%	76,452	10.3%	*0.02*	*0.39*	*0.01*
	TS: 3x3	-	-	-	[c]	-	-	76,511	10.3%	*0.25*	*0.50*	-
	TS: 3x2	-	-	-	76,555	6,410	10.4%	76,506	10.3%	*0.25*	*0.92*	*0.16*
	TS: 3x2*	-	-	-	76,257	6,383	10.0%	76,480	10.3%	*0.25*	*0.39*	*0.11*
	TS: 2x2	-	-	-	76,579	6,512	10.4%	76,508	10.3%	*0.22*	*0.92*	-
	TS: 2x2*	-	-	-	75,742	6,530	9.2%	76,454	10.3%	*0.22*	*0.39*	-

[a] P = pooled, T = temporal, TS - temporal by spatial; see Table 17 for strata definitions. For *a* x *b* strata, *a* refers to application and *b* refers to recovery. Pooling scenarios are:

Temporal:	All x 4 (1,2,3,4+5)	All x 2 (1+2,3+4+5)	3 (1,2+3,4+5) x All
	All x 3 (1+2,3,4+5)	4 (1,2,3,4+5) x All	2 (1+2+3,4+5) x All
Temporal/Spatial:	All x 3 (1,2,3)	All x 2* (1,2+3)	3 (1,2,3+4,5) x All
	All x 2 (1+2,3)	4 (1,2,3+4,5) x All	2 (1+2,3+4+5) x All

[b] Mark-recapture estimate (+ above; - below) vs best estimate of escapement (64,843 males and 69,343 females).

[c] ML Darroch estimator failed to produce an estimate.

Table 8b. Escapement estimates for 1994 Stellako River sockeye males and females calculated using Petersen, Darroch and Schaefer estimators under various stratification and pooling scenarios: *enumeration fence recovery data only*

		Petersen estimator			ML Darroch estimator			Schaefer estimator		*SPAS Test Results*		
Sex	Pooling [a]	Estimate	+/- 95% cl	% Dev [b]	Estimate	+/- 95% cl	% Dev [b]	Estimate	% Dev [b]	*Complete mixing*	*Equal propns*	*Plante's G^2*
Male	P: 1x1	53,320	8,480	-17.8%	-	-	-	-	-	-	-	-
	T: 5x5	-	-	-	[c]	-	-	53,041	-18.2%	*0.00*	*0.40*	-
	T: 5x4	-	-	-	[c]	-	-	53,447	-17.6%	*0.00*	*0.27*	-
	T: 5x3	-	-	-	53,271	13,072	-17.8%	53,457	-17.6%	*0.00*	*0.14*	*0.00*
	T: 5x2	-	-	-	52,839	10,165	-18.5%	53,581	-17.4%	*0.00*	*0.78*	*0.00*
	T: 4x4	-	-	-	[c]	-	-	52,853	-18.5%	*0.00*	*0.27*	-
	T: 4x3	-	-	-	[c]	-	-	52,801	-18.6%	*0.00*	*0.14*	-
	T: 4x2	-	-	-	[c]	-	-	53,455	-17.6%	*0.00*	*0.78*	-
	T: 3x3	-	-	-	[c]	-	-	52,977	-18.3%	*0.00*	*0.14*	-
	T: 3x2	-	-	-	[c]	-	-	53,418	-17.6%	*0.00*	*0.78*	-
	T: 2x2	-	-	-	52,312	12,520	-19.3%	53,429	-17.6%	*0.00*	*0.78*	-
Female	P: 1x1	95,356	20,927	37.5%	-	-	-	-	-	-	-	-
	T: 5x5	-	-	-	[c]	-	-	100,768	45.3%	*0.00*	*0.01*	-
	T: 5x4	-	-	-	[c]	-	-	100,766	45.3%	*0.00*	*0.01*	-
	T: 5x3	-	-	-	[c]	-	-	99,875	44.0%	*0.00*	*0.00*	-
	T: 5x2	-	-	-	118,381	35,627	70.7%	102,069	47.2%	*0.00*	*0.06*	*0.23*
	T: 4x4	-	-	-	[c]	-	-	100,764	45.3%	*0.00*	*0.01*	-
	T: 4x3	-	-	-	[c]	-	-	99,873	44.0%	*0.00*	*0.00*	-
	T: 4x2	-	-	-	118,381	35,609	70.7%	102,069	47.2%	*0.00*	*0.06*	*0.12*
	T: 3x3	-	-	-	[c]	-	-	100,778	45.3%	*0.00*	*0.00*	-
	T: 3x2	-	-	-	118,184	35,335	70.4%	102,096	47.2%	*0.00*	*0.06*	*0.70*
	T: 2x2	-	-	-	118,292	35,488	70.6%	101,091	45.8%	*0.00*	*0.06*	-

[a] P = pooled, T = temporal, TS - temporal by spatial; see Table 17 for strata definitions. For *a* x *b* strata, *a* refers to application and *b* refers to recovery. Pooling scenarios are:

Temporal:			
	All x 4 (1,2,3,4+5)	All x 2 (1+2,3+4+5)	3 (1,2+3,4+5) x All
	All x 3 (1+2,3,4+5)	4 (1,2,3,4+5) x All	2 (1+2+3,4+5) x All

[b] Mark-recapture estimate (+ above; - below) vs best estimate of escapement (64,643 males and 69,343 females).

[c] ML Darroch estimator failed to produce an estimate.

from ±11% to ±19%. None of the MLE estimates improve on or are within 1% of the already highly accurate PPE estimate. Overall, the MLE estimates the population with errors ranging from -12% to +14%; the 95% CI's of all of the estimates include the known study area population. Among the 17 female stratifications that produce estimates, the SPAS complete mixing, equal proportions, and Plante's G^2 test results exceed 0.05 in 2, 16, and 10 cases, respectively. The female estimates are both robust to pooling and precise: the estimates range from 77,749 to 81,720; and the 95% CI's range from ±6% to ±8%. Seven of the stratifications produce estimates that improve on the accuracy of the PPE by at least 1%, six produce estimates that are within 1%, and four increase the error (to 18%). Overall, the MLE estimates the population with a positive bias of 12% to 18%; none of the 95% CI's include the known study area population.

Estimator Selection

MLE Estimates: For most data sets, the MLE produces population estimates that improve the accuracy of the PPE under certain stratification and pooling scenarios. Conversely, it also produces estimates with substantially greater error under other pooling scenarios. At issue, then, is identifying the attributes of the former so as to minimize the risk of selecting the latter. In Figure 4, I show the relationship between the accuracy of an MLE estimate and three attributes potentially associated with its accuracy: the G^2 test result, the

Table 8c. Escapement estimates for 1994 Stellako River sockeye males calculated using Petersen, Darroch and Schaefer estimators under various stratification and pooling scenarios: *aggregate recovery data*.

		Petersen estimator			ML Darroch estimator			Schaefer estimator		*SPAS Test Results*		
Sex	Pooling [a]	Estimate	+/- 95% cl	% Dev [b]	Estimate	+/- 95% cl	% Dev [b]	Estimate	% Dev [b]	*Complete mixing*	*Equal propns*	*Plante's* G^2
Male	P: 1x1	64,265	5,477	-0.9%	-	-	-	-	-	-	-	-
	T: 5x5	-	-	-	[c]	-	-	64,610	-0.4%	*0.00*	*0.00*	-
	T: 5x4	-	-	-	[c]	-	-	64,591	-0.4%	*0.00*	*0.00*	-
	T: 5x3	-	-	-	[c]	-	-	64,449	-0.6%	*0.00*	*0.00*	-
	T: 5x2	-	-	-	60,567	6,565	-6.6%	64,156	-1.1%	*0.00*	*0.00*	*0.01*
	T: 4x4	-	-	-	[c]	-	-	64,508	-0.5%	*0.00*	*0.00*	-
	T: 4x3	-	-	-	[c]	-	-	64,387	-0.7%	*0.00*	*0.00*	-
	T: 4x2	-	-	-	60,433	6,601	-6.8%	64,140	-1.1%	*0.00*	*0.00*	*0.01*
	T: 3x3	-	-	-	[c]	-	-	64,374	-0.7%	*0.00*	*0.00*	-
	T: 3x2	-	-	-	[c]	-	-	64,126	-1.1%	*0.00*	*0.00*	-
	T: 2x2	-	-	-	57,214	9,224	-11.8%	64,109	-1.1%	*0.01*	*0.00*	-
	TS: 5x4	-	-	-	[c]	-	-	66,115	2.0%	*0.00*	*0.01*	-
	TS: 5x3	-	-	-	[c]	-	-	65,747	1.4%	*0.00*	*0.01*	-
	TS: 5x3*	-	-	-	73,784	13,639	13.8%	66,049	1.9%	*0.00*	*0.00*	*0.92*
	TS: 5x3**	-	-	-	[c]	-	-	65,948	1.7%	*0.00*	*0.01*	-
	TS: 5x2	-	-	-	67,263	7,135	3.7%	65,223	0.6%	*0.00*	*0.02*	*0.16*
	TS: 5x2*	-	-	-	69,649	8,709	7.4%	65,579	1.1%	*0.00*	*0.01*	*0.61*
	TS: 4x4	-	-	-	[c]	-	-	66,113	2.0%	*0.00*	*0.01*	-
	TS: 4x3	-	-	-	[c]	-	-	65,745	1.4%	*0.00*	*0.01*	-
	TS: 4x3*	-	-	-	74,105	14,251	14.3%	66,047	1.9%	*0.00*	*0.00*	*0.83*
	TS: 4x3**	-	-	-	[c]	-	-	65,946	1.7%	*0.00*	*0.01*	-
	TS: 4x2	-	-	-	67,252	7,163	3.7%	65,222	0.6%	*0.00*	*0.02*	*0.08*
	TS: 4x2*	-	-	-	69,734	8,711	7.5%	65,577	1.1%	*0.00*	*0.01*	*0.42*
	TS: 3x3	-	-	-	[c]	-	-	65,763	1.4%	*0.00*	*0.01*	-
	TS: 3x3*	-	-	-	[c]	-	-	66,061	1.9%	*0.00*	*0.00*	-
	TS: 3x3**	-	-	-	[c]	-	-	65,953	1.7%	*0.00*	*0.01*	-
	TS: 3x2	-	-	-	[c]	-	-	65,243	0.6%	*0.00*	*0.02*	-
	TS: 3x2*	-	-	-	70,625	9,812	8.9%	65,589	1.2%	*0.00*	*0.01*	*0.67*
	TS: 2x2	-	-	-	69,157	8,540	6.7%	65,153	0.5%	*0.00*	*0.02*	-
	TS: 2x2*	-	-	-	70,807	10,014	9.2%	65,387	0.8%	*0.00*	*0.01*	-

[a] P = pooled, T = temporal, TS - temporal by spatial; see Table 17 for strata definitions. For *a* x *b* strata, *a* refers to application and *b* refers to recovery. Pooling scenarios are:

Temporal:	All x 5 (1,2,3,4,5+6)	4 (1,2,3,4+5) x All
	All x 4 (1+2,3,4,5+6)	3 (1,2+3,4+5) x All
	All x 3 (1+2,3,4+5+6)	All x 2 (1+2,3-6)
Temporal/Spatial:	All x 3 (1+2,3,4)	All x 2* (1+2,3+4)
	All x 3* (1,2+3,4)	4 (1,2,3+4,5) x All
	All x 3** (1,2,3+4)	3 (1,2,3+4+5) x All
	All x 2 (1+2+3,4)	2 (1+2,3+4+5) x All

[b] Mark-recapture estimate (+ above; - below) vs best estimate of escapement (64,843 males).

[c] ML Darroch estimator failed to produce an estimate.

Table 8d. Escapement estimates for 1994 Stellako River sockeye females calculated using Petersen, Darroch and Schaefer estimators under various stratification and pooling scenarios: *aggregate recovery data.*

		Petersen estimator			ML Darroch estimator			Schaefer estimator		*SPAS Test Results*		
Sex	Pooling [a]	Estimate	+/- 95% cl	% Dev [b]	Estimate	+/- 95% cl	% Dev [b]	Estimate	% Dev [b]	*Complete mixing*	*Equal propns*	*Plante's* G^2
Female	P: 1x1	80,717	5,058	16.4%	-	-	-	-	-	-	-	-
	T: 5x5	-	-	-	[c]	-	-	80,836	16.6%	*0.03*	*0.10*	-
	T: 5x4	-	-	-	[c]	-	-	80,822	16.6%	*0.03*	*0.06*	-
	T: 5x3	-	-	-	[c]	-	-	80,836	16.6%	*0.03*	*0.13*	-
	T: 5x2	-	-	-	80,476	5,222	16.1%	80,794	16.5%	*0.03*	*0.68*	*0.02*
	T: 4x4	-	-	-	[c]	-	-	80,803	16.5%	*0.02*	*0.06*	-
	T: 4x3	-	-	-	[c]	-	-	80,821	16.6%	*0.02*	*0.13*	-
	T: 4x2	-	-	-	80,444	5,301	16.0%	80,798	16.5%	*0.02*	*0.68*	*0.01*
	T: 3x3	-	-	-	[c]	-	-	80,832	16.6%	*0.09*	*0.13*	-
	T: 3x2	-	-	-	80,521	5,238	16.1%	80,795	16.5%	*0.09*	*0.68*	*0.04*
	T: 2x2	-	-	-	80,266	5,633	15.8%	80,789	16.5%	*0.11*	*0.68*	-
	TS: 5x4	-	-	-	81,720	6,429	17.8%	80,610	16.2%	*0.03*	*0.09*	*0.37*
	TS: 5x3	-	-	-	80,124	5,455	15.5%	80,539	16.1%	*0.03*	*0.08*	*0.32*
	TS: 5x3*	-	-	-	81,451	6,088	17.5%	80,640	16.3%	*0.03*	*0.06*	*0.65*
	TS: 5x3**	-	-	-	81,669	6,400	17.8%	80,708	16.4%	*0.03*	*0.22*	*0.65*
	TS: 5x2	-	-	-	79,443	5,106	14.6%	80,549	16.2%	*0.03*	*0.03*	*0.11*
	TS: 5x2*	-	-	-	79,768	5,178	15.0%	80,637	16.3%	*0.03*	*0.21*	*0.44*
	TS: 4x4	-	-	-	[c]	-	-	80,612	16.3%	*0.01*	*0.09*	-
	TS: 4x3	-	-	-	80,145	5,484	15.6%	80,539	16.1%	*0.01*	*0.08*	*0.14*
	TS: 4x3*	-	-	-	81,512	6,169	17.5%	80,641	16.3%	*0.01*	*0.06*	*0.43*
	TS: 4x3**	-	-	-	[c]	-	-	80,711	16.4%	*0.01*	*0.22*	-
	TS: 4x2	-	-	-	79,445	5,107	14.6%	80,549	16.2%	*0.01*	*0.03*	*0.05*
	TS: 4x2*	-	-	-	79,763	5,180	15.0%	80,638	16.3%	*0.01*	*0.21*	*0.26*
	TS: 3x3	-	-	-	[c]	-	-	80,615	16.3%	*0.01*	*0.08*	-
	TS: 3x3*	-	-	-	[c]	-	-	80,716	16.4%	*0.01*	*0.06*	-
	TS: 3x3**	-	-	-	[c]	-	-	80,729	16.4%	*0.01*	*0.22*	-
	TS: 3x2	-	-	-	[c]	-	-	80,625	16.3%	*0.01*	*0.03*	-
	TS: 3x2*	-	-	-	79,586	5,274	14.8%	80,657	16.3%	*0.01*	*0.21*	*0.13*
	TS: 2x2	-	-	-	77,749	6,126	12.1%	80,677	16.3%	*0.03*	*0.03*	-
	TS: 2x2*	-	-	-	79,794	5,219	15.1%	80,701	16.4%	*0.03*	*0.21*	-

[a] P = pooled, T = temporal, TS - temporal by spatial; see Table 17 for strata definitions. For *a* x *b* strata, *a* refers to application and *b* refers to recovery. Pooling scenarios are:

Temporal:	All x 5 (1,2,3,4,5+6)	All x 2 (1+2,3-6)
	All x 4 (1+2,3,4,5+6)	4 (1,2,3,4+5) x All
	All x 3 (1+2,3,4+5+6)	3 (1,2+3,4+5) x All
Temporal/Spatial:	All x 3 (1+2,3,4)	All x 2* (1+2,3+4)
	All x 3* (1,2+3,4)	4 (1,2,3+4,5) x All
	All x 3** (1,2,3+4)	3 (1,2,3+4+5) x All
	All x 2 (1+2+3,4)	2 (1+2,3+4+5) x All

[b] Mark-recapture estimate (+ above; - below) vs best estimate of escapement (69,343 females).

[c] ML Darroch estimator failed to produce an estimate.

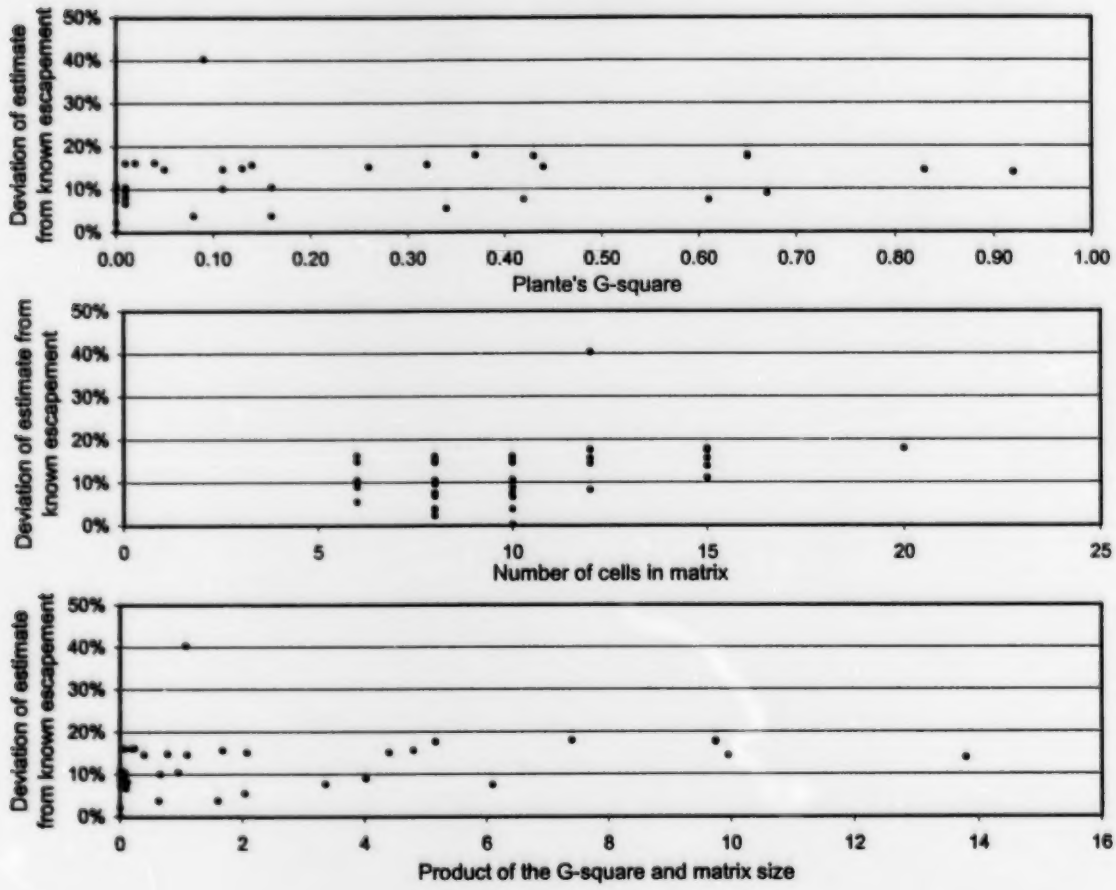

Figure. 4. MLE escapement estimate error versus the p-value of the G^2 test, the number of cells in the matrix, and the product of the p-value and matrix size, for escapements estimated from spawning ground and aggregate recoveries.

extent to which the data are pooled, and the product of the two as a simple approximation of their joint maximization. None of these attributes is associated with accuracy; an estimate with a large G^2 test result is no more accurate than one with a small result, and average accuracy is actually better when $G^2 < 0.05$ (10% error) than when $G^2 > 0.05$ (14% error). Similarly, there is no indication that accuracy is related to the degree of pooling, or can be improved by the joint maximization of the G^2 and matrix size. Consequently, none of these attributes are useful in decision rules for selecting the best MLE estimate. No other obvious criteria are available.

Best Estimator: There are also no rigorous criteria available to guide in the selection of the most appropriate estimator among the PPE, MLE and Schaefer. The Schaefer does not substantially improve the accuracy of the PPE in any of the stratifications or data sets tested (Table 8). While the MLE in many cases is more accurate than the PPE, there is no rigorous way to discriminate between the pooling scenarios that produce more accurate estimates from those that produce less accurate estimates. Consequently, rejecting a PPE in favour of an MLE estimate to address data biases entails a risk that a less accurate estimate will be adopted. The male MLE estimates in Table

8a exemplify this risk. If I follow the procedures of previous reports (see Methods), the T:4×3 and TS:5×2 matrices are equally likely to be selected depending on whether I initially stratify the data in temporal:temporal or temporal:spatial matrices. If I reject the PPE, selection of the former increases the error from 17.5% to 40.3%, while selection of the latter reduces it to 0.2%. These results are extreme because the data set is not robust to pooling; however, similar but less extreme results are produced when the procedure is applied to the other data sets in tables 8a, 8c and 8d.

DISCUSSION

I address four questions in this section. Is the study area escapement estimate, *i.e.*, the estimate based on the fence count, a useful metric to evaluate mark-recapture accuracy? Are the mark-recapture estimates biased and, if so, what role is played by stress and sampling selectivity? Can stratification and pooling improve the accuracy of the mark-recapture estimates? Are the study results and conclusions transferable to other projects?

WAS THE 'FENCE' ESTIMATE ACCURATE?

Before discussing the issue of estimation accuracy, I will first review the components of the study area population to determine whether it is a valid benchmark against which the mark-recapture estimates can be evaluated. The components include fish counted at the fence that spawned in the Nadina system, those already in the Stellako River when the fence was installed (the fence count itself is considered a complete census of immigration from early in the run until its completion), and sex composition of the population. I calculated the Nadina component from the known tagging rate at the fence and an almost complete examination of Nadina sockeye for tags; consequently, sample size does not constrain the accuracy of the estimate. The estimate would be biased, however, if tagged fish migrated to other upstream spawning areas (unlikely because negligible escapements were reported in other areas (Schubert 1998)), if tagging stress induced Nadina fish to remain in the Stellako River, or if the tag rate was inaccurate. That some fish were unable to migrate further upstream is evident from the 16 tagged carcasses that were recovered at the fence or in the lower river shortly after release. Even if these fish were recovered at the study area average rate of 61% (probably higher if they were more likely to be recovered on the fence) and if untagged fish were completely unstressed (probably untrue), the Nadina component would be underestimated by less than five fish. I estimated tag rate from the study period average rather than from an early component of the run when Nadina sockeye were most likely present because, without a record of tag numbers at Nadina, I was unable to identify their period of presence. Because the tag rate early in the run was below the average, the Nadina component may have been underestimated. For example, if the Nadina migration was complete by September 10, the underestimate would be 58 fish. Consequently, the impact of both stress and tag rate on the study area escapement estimate is trivial. The estimate of the number of Nadina fish counted at the fence (198) is consistent with size of the Nadina escapement, which is small (2,097) relative to the fence count (121,525). Further, the estimate is also consistent with a short overlap in the migration of Stellako and Nadina sockeye, as shown by data collected at a fence installed at the Francois Lake outlet in 1953 (IPSFC, unpublished data).

The second component of the study area population is an estimate of the number of sockeye already in the river when the fence was installed. The reliability of this estimate depends on the accuracy of a single live count and the appropriateness of the analytic procedure. The former was a count of sockeye clustered in the upper river in small, easily observed groups that was conducted under the ideal conditions of clear water, sunshine and still air. Consequently, the count was at the upper end of the reliability range for visual observations. The latter is an IPSFC procedure developed for cyclic surveys conducted during the period of initial arrival through peak spawning. Three assumptions are implicit: visual counts always have a negative bias; spawner turn-over will occur, *i.e.*, the peak observation is preceded by die-off and followed by the arrival of additional spawners; and live fish are counted under average viewing conditions. The latter two assumptions are violated in this study. Spawner turn-over did not occur because holding rather than spawning fish were counted, and viewing conditions were optimal rather than average. Both likely introduced a positive bias, with the true population size likely bounded by the estimate (13,032) and the obser-

vation (7,250). The total study area escapement of 134,186, then, is likely estimated with a maximum probable error of +4%.

The final component is an estimate of the sex composition of the escapement. Two data sources were available: the ratios of the sex-specific PPE estimates; and the sex ratios among recovered carcasses. I rejected the former because of variability among the two sets of PPE estimates (the male proportion ranges from 36% to 50%). I also rejected the individual spawning ground and fence samples because stress effects (Table 5) and selectivity (Table 6) are sex-specific. Instead, I used the sex ratio from the aggregate carcass recovery. The sample is large (61% of the estimate) and includes all carcasses except those that settled into deep pools, were removed by predators, or decomposed between surveys; overall, such processes are unlikely to be sex-specific.

Given the above, I conclude that the sex-specific study area escapement estimate is a reasonable approximation of the study area population. It should permit the identification of mark-recapture estimation errors that exceed 4% of the true population size.

WERE THE MARK-RECAPTURE ESTIMATES BIASED?

My focus in this section is the accuracy of the PPE estimates calculated from spawning ground and aggregate recoveries. Fence recoveries are excluded because, under normal field conditions, they would never be used in isolation to generate PPE estimates (although they play a central role in evaluating stress and selectivity; discussed later). With one exception (males estimated from aggregate recoveries), the PPE produces relatively inaccurate estimates, with errors ranging from 10% to 18% and confidence limits that do not include the known escapement. This occurred despite a study design that permitted (but did not achieve) proportional tagging as well as very high recovery rates, indicating that one or more of the assumptions underlying the mark-recapture technique were violated. These include the assumptions that: the population is closed; tags are correctly identified at recapture; tags are not lost between capture and recapture; capture probabilities are equal for all fish; and recapture probabilities are independent of tag status. The two former assumptions are met in this study: the population is closed because there was no emigration past the fence, and virtually all fish that migrated above the study area were examined for tags; and tag identification error, although present, was corrected using the resurvey data. It is the evaluation of tag loss and sampling probabilities (especially the role of stress in the latter) then, that is central to determining the source of PPE estimation error.

Tag Loss

The undetected loss of tags between application and recovery results in an underestimate of the proportion of the population with tags and an overestimate of escapement. If present, tag loss was undetected because secondary marks or tags were not used; consequently, undetected tag loss may in part explain the positive bias in three of the four PPE estimates. I can infer the probable range of tag loss (and its role in PPE error) from other sources. The source most directly applicable is a double tagging study conducted on Fraser River sockeye in 1989 (DFO, unpublished) that reports an average tag loss of 3.5%, and a range among studies of 0% to 9.7%. I illustrate the estimation error that would occur over this range by recalculating the PPE's from data adjusted for tag loss (Fig. 5). Tag loss in this range improves the accuracy of the sexes-combined population estimate because tag loss results in overestimates and three of the four sex-specific population estimates had positive biases of at least 10%. At the 3.5% average loss reported in 1989, overall accuracy improves by about 4%, but the error remains substantial (6.3% to 13.4%). Even at the high end of the range (9.7%), error exceeds 5% in the male spawning ground and female aggregate estimates and increases to 10.5% in the previously accurate male aggregate estimate. These results suggest that the failure to assess tag loss contributes to the observed estimation error, but that tag loss alone does not fully explain the magnitude of that error.

Stress And Sampling Selectivity

The capture, holding and tagging of fish can subject them to physiological stress (Ricker 1975). The impact of stress on estimator accuracy can be insidious because it is often difficult or impossible to distinguish between the effects of stress and sampling biases at capture or recapture. For

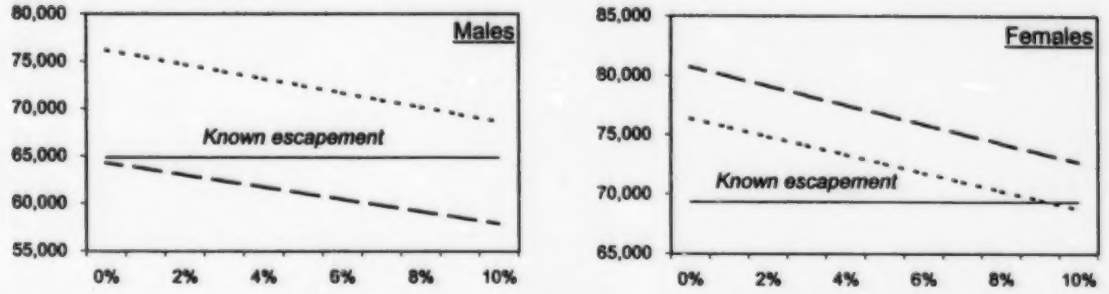

Figure 5. PPE population estimates relative to the known escapement at tag loss rates ranging from 0% to 10%. The finely dashed line represents estimates calculated from spawning ground recoveries; the coarsely dashed lines represent estimates calculated from aggregate recoveries.

example, stress can influence the distance and duration of migration by impairing swimming ability and causing an earlier death, while selective capture can have similar effects by favouring fish with specific spawning distributions or schedules. The failure to correctly identify stress effects can induce estimation error because unique mechanisms underlie each process and each requires different corrective measures. With selectivity, the bias tests should be effective when selectivity is present at the level necessary to bias the population estimates. The bias can then (in theory) be corrected by using a stratified population estimator. With stress, the population estimates can be highly biased even when the stress effects are present at a level below the threshold for detection by the bias tests. When detected, stress effects can be corrected by removing the affected individuals from the data set. They can, however, be easily confused with sampling selectivity, an important concern because stratification cannot mitigate for stress-induced changes in the recovery probability of a tagged fish. Corrective action will not improve the accuracy of extremely biased population estimates, therefore, unless the underlying cause of the bias is correctly identified. In the current study, the fence provides an independent estimate of the study area population against which the mark-recapture estimates can be compared. Equally importantly, it also provides an estimate of the total (and daily) number of untagged sockeye entering the study area, and the number, sex and tag status of the carcasses that would otherwise have been flushed downstream. The former provides a powerful tool to investigate the underlying mechanism for estimation bias because it permits the calculation of sex-specific recovery rates for tagged and untagged sockeye. The latter provides insights into the mechanisms causing differential recovery, and the respective roles of sampling selectivity and stress.

The PPE estimates from spawning ground recoveries are 18% and 10% larger than the study area populations of males and females, respectively (Table 8a). Even considering unassessed tag loss and the potential bias in the study area population estimate, differences of this magnitude indicate the presence of stress or selectivity that should have been detectable by the bias tests. In fact, my evaluation of the spawning ground recoveries detected little evidence of stress (Table 5) and only a temporal recovery bias in one sample (Table 6) that would not be expected to bias the population estimates. That the bias was positive is contrary to expectation; declining tag incidence with time and declining recovery rate with time (Fig. 6) would suggest a negative rather than positive bias. What, then, was the source of the error? The answer is simple; it results from a lower probability of recovery of tagged versus untagged sockeye. Recovery rates are 4-5% lower among tagged fish. This differential is stable except at very high levels of tag loss among males; it disappears among females at very high (and probably unrealistic) rates of tag loss (Fig. 5). An examination of the spawning ground and fence data provides insights into these differences, and suggests that unique mechanisms affect each sex.

Among males, tagged fish were recovered at a higher rate (than untagged fish) at the fence but a lower rate on the spawning grounds, with the difference largely disappearing when the samples

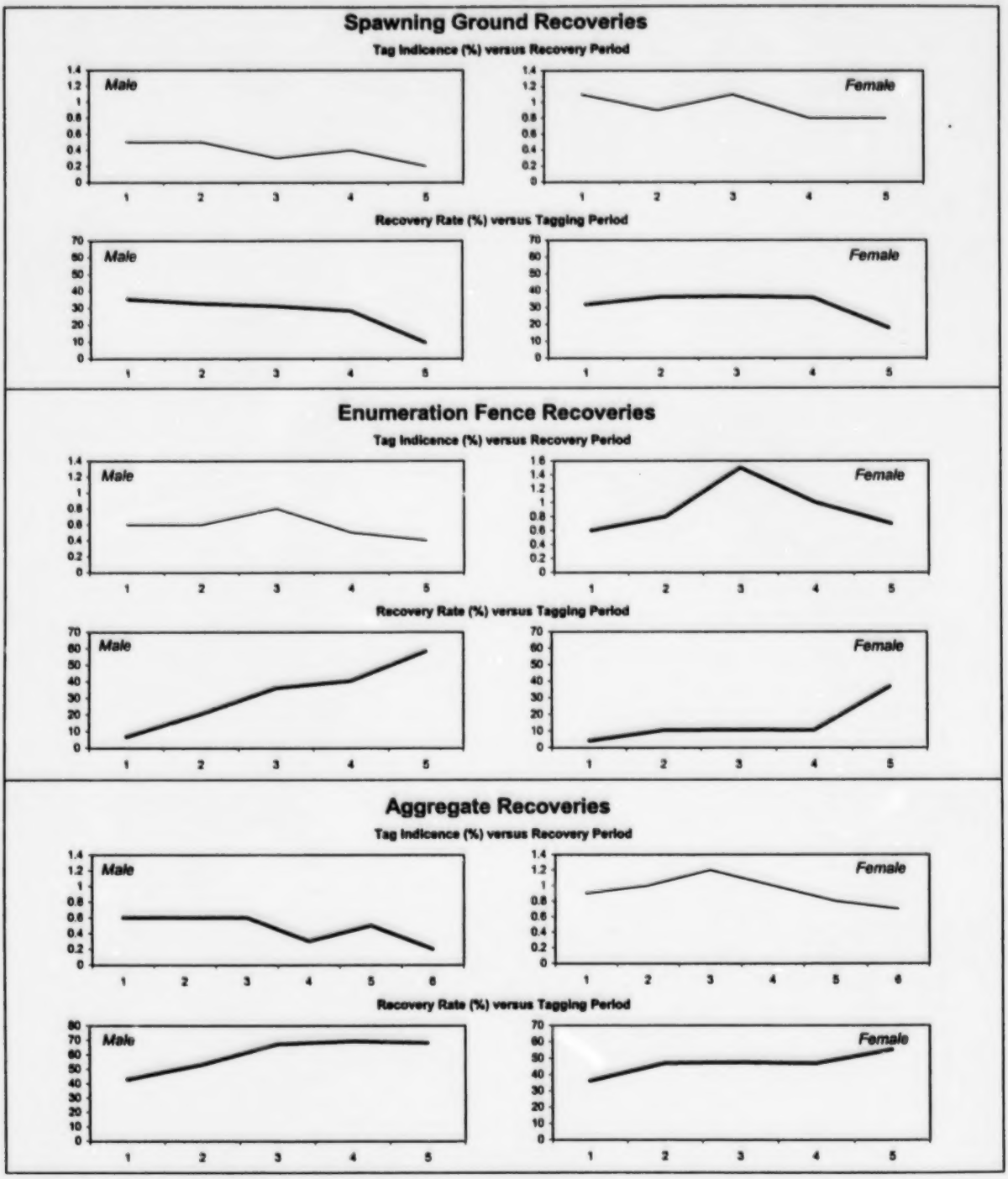

Figure 6. Tag incidence across recovery periods, and recovery rate across application periods, for Stellako River male and female sockeye tagged at the fence and recovered on the spawning grounds, at the fence and in aggregate. Bold lines indicate significant differences ($P > 0.05$; chi-square) among periods. Data are from appendices 10-11, *'Similar numbers of tags applied'* or *'Similar total recoveries.'*

Table 9. Study area population size, and recovery rates on the spawning grounds, at the enumeration fence, and in aggregate at three levels of tag loss, by sex and tag status. The symbols * and ** indicate chi-square test results that are significant (P< 0.05) and highly significant (P < 0.005), respectively.

Population size and recovery rate	Male		Female		Total	
	Tagged	Untagged	Tagged	Untagged	Tagged	Untagged
Study area population	320	64,523	863	68,480	1,183	133,003
Recovery rate at three levels of tag loss: [a]						
Spawning Grounds						
0% tag loss	30%	35%	39%	43% *	37%	39%
3.5% tag loss	31%	35%	41%	43%	38%	39%
9.7% tag loss	34%	35%	44%	43%	41%	39%
Enumeration fence [b]						
0% tag loss	45%	40%	22%	33% **	29%	37% **
3.5% tag loss	47%	40% *	23%	33% **	30%	37% **
9.7% tag loss	50%	40% **	25%	33% **	32%	37% *
Aggregate						
0% tag loss	62%	61%	53%	62% **	55%	61% **
3.5% tag loss	64%	61%	55%	62% **	57%	61% **
9.7% tag loss	69%	61% *	58%	61%	61%	61%

[a] Lower and upper limits and mean of tag loss range reported by 1989 Fraser River sockeye studies (DFO, unpublished).

[b] The product of: fish recovered on the fence; and the study area population minus spawning ground recoveries.

are combined. In other words, tagged males were more likely to be flushed from the study area. The available evidence suggests that the mechanism is a stresser that impairs swimming ability and decreases post-tagging life spans (*i.e.*, causes an earlier death). Male spawning ground behaviour is less redd-oriented and, consequently, males have a higher probability of drifting downstream and a lower probability of recovery on the shore. An acute (or even subacute) stresser may have exacerbated this behaviour among tagged fish. That swimming performance was impaired by stress is supported by the progressively lower tag incidence with distance upstream. A shorter post-tagging lifespan is supported by a shorter time out to recovery (by almost half) among males recovered at the fence compared to in the river. The time between river entry and recovery was also shorter for tagged fish (Fig. 3); however, this evidence is weak because the data are not sex-specific.

In contrast to males, tagged females were recovered at a lower rate (than untagged females) both at the fence and on the spawning grounds. The difference among aggregate recoveries is very large and is not eliminated at probable levels of tag loss (Table 10). This is inconsistent with stress because it would change the probability of recovery of tagged fish in the first (spawning ground) sample and, consequently, have the opposite effect in the second (fence) sample simply because greater (or fewer) numbers of tagged fish would be available for recovery. Among females, the recovery rates of tagged fish are lower in both samples, *i.e.*, unlike males, tagged females were not flushed from the study area. While there is evidence that females were affected by stress, it is not overwhelming when considered in the context of all available information. Like males, there was a shorter time out to recovery among females recovered at the fence compared to in the river, suggesting a shorter life span. Spawning success among fence recoveries was lower than river recoveries in both tagged and untagged fish, suggesting that stress may have impaired the spawning ability of the females most likely to be flushed from the study area. Other evidence, however, is inconsistent with the presence of a serious stressor. Tag rates did not decline with distance upstream, and a high proportion of the recoveries were in the upper river (Appendix 12). This suggests that swimming performance was unimpaired and females were more capable of lengthy upstream migrations regardless of tag status. Furthermore, the spawning success of tagged and untagged females was essentially the same. If present, the effect of stress on females may be subacute, *i.e.*, it may be manifested in subtle be-

havioural changes that influence subsequent catchability but that do not affect the ability of the fish to migrate through the river and to spawn successfully.

Excluding stress, what other mechanism might explain the lower probability of recovery of tagged females both among fish vulnerable to the river surveys and those that otherwise would have been flushed from the study area? The apparent probability of recovery of tagged females would be lower (if the processes are sex-specific) when: tag loss occurs at a high rate; predators key on tagged fish; tagged fish have a higher probability of sinking into pools; or technicians are less likely to recognize the status of tagged fish. Tag loss, while unassessed in this study, was documented among Fraser River sockeye stocks in 1989 and, more recently, in 1998. Tag loss varied substantially between sexes with no obvious mechanism to explain higher tag loss in one sex or the other. It is possible, therefore, that Stellako females lost tags at a higher rate than males. Predation by bears may reduce the probability of recovery of tagged females. Bears have been observed sorting catch (*i.e.*, catching and releasing live fish) to enable them to preferentially harvest females. In the Stellako River, this mechanism would reduce the recoverability of tagged females if the tag made the fish more obvious to a bear. It would also reduce recoverability if subacute stress caused tagged females to select redd sites in slower flowing, peripheral areas because they were less able to hold station in faster currents. The loss of carcasses in deep pools almost certainly occurs. A bias would be introduced if stress caused tagged females to hold and die in pools; however, there is no reason to believe the carcasses of such fish would be retained in the pools. And finally, tag recognition may be reduced among female carcasses because females tend to hold station on redds longer than males, possibly causing greater decomposition and fungal infestation (that obscures tag recognition) by the time they die. The resurvey showed that substantially more tagged females were misidentified as untagged in the initial survey (Appendix 7). This would reduce the apparent probability of recovery, however, only if the resurvey was non-representative or if tag recognition was also impaired on the resurvey. In this study, the resurvey examined 46% of the recovered carcasses and, with the exception of the first eight days of the recovery, was representative both temporally and spatially. Study design, therefore, should not have been a factor in 1994. In conclusion, there are several possible mechanisms that could explain the observed differential recovery among females. With the current data, it is not possible to evaluate the relative role of these mechanisms, or even whether they were present. Future studies must ensure that tag loss is assessed and the resurvey is representative. They should also consider applying standard and low visibility tags to investigate whether tag recognition, both by predators and technicians, plays a role in changing recovery probabilities.

This study highlights the central role played by tag loss and stress in mark-recapture estimation accuracy. Tag loss clearly must be assessed to minimize bias and permit the assessment of behavioural factors that can result in the differential recovery of marked fish. This study demonstrates that different mechanisms can affect each sex, and stress (acute of subacute) can play a role in both sexes. It is important to note that, while stress was almost certainly associated with the differential probability of recovery of tagged males, it was undetected by the standard stress tests. Because stress impacts can be insidious, mark-recapture studies must be designed to minimize capture and handling stress if they are to avoid producing biased population estimates.

DID STRATIFICATION IMPROVE ACCURACY?

A variety of stratified population estimators have become more accessible with the development of computer software such as SPAS (Arnason *et al.* 1996) and MARK (White and Burnham 1997). Such packages vastly increase the analytic capabilities of experimenters in this field. They raise the question, however, of when to use the PPE and, if a stratified estimator is selected, which one should be used and under what stratification scheme. Other 1994 Fraser River sockeye mark-recapture studies use a simple procedure to choose between the PPE and MLE population estimates. If the sampling selectivity tests show no evidence of bias, the PPE is used. If sampling bias is detected, the 95% confidence limits of the PPE and MLE are compared. If there is overlap, the bias is judged to be minor and the PPE is accepted; if there is no overlap, the MLE is accepted as the most appropriate es-

timator. The basic assumption underlying this procedure is that, in the face of biased data sets, stratification and pooling will improve estimation accuracy relative to that of the PPE. The results of this study show that this assumption may not be valid.

In this study, I calculate 116 Schaefer and MLE estimates using different stratification and pooling schemes. A comparison of these estimates with the study area population provides two useful insights. First, the Schaefer estimator provides estimates that are both similar to the PPE and robust to pooling (Table 8). If the data are sufficiently biased to bias the PPE estimate, therefore, the Schaefer will not substantially improve the accuracy of the estimate, and the exploration of alternate pooling schemes will not provide useful information. In fact, estimator stability across pooling scenarios may increase one's confidence in an estimate that is in fact highly biased. Amason (University of Manitoba, pers. comm.) notes that the Schaefer estimator is useful only under the same conditions as the PPE, in which case the latter should be used to maximize precision. Second, the MLE can provide estimates that improve on the accuracy of the PPE. Unfortunately, there is no obvious way to discriminate between pooling scenarios that improve estimation accuracy and those that exacerbate the error. The MLE can be effective when the data have a strongly diagonal structure, *i.e.*, a temporal correlation between application and recovery strata (C. Schwarz, Simon Fraser University, pers. comm.). This is not the case with typical sockeye mark-recapture studies because there is considerable mixing of tags across recovery strata. There is a non-trivial risk, therefore, that the use of the ML Darroch estimator will introduce considerable bias in a population estimate.

If the available stratified population estimators cannot be relied on to improve estimation accuracy when biases are detected, what estimation procedure should be used? Clearly, further work is required to develop a MLE suited to sockeye mark-recapture studies. As an interim measure, I recommend adopting the PPE as the primary population estimator; however, the estimates should be qualified based on a subjective evaluation of the data. There are at least two ways such an evaluation could be performed. On a relatively gross and subjective level, one could evaluate the design and execution of the study. Did tagging begin when sockeye first arrived and continue until the migration was complete? Did recovery begin shortly after the start of tagging, cover the entire study area, and continue until the die-off was complete? Was the tagging and recovery effort applied representatively over time and space? Were lost and missed tags reliably assessed? If the answer to these questions is yes, then the study was adequately designed and executed and the estimates are reasonable approximations of population size. Such an evaluation would conclude that the Stellako study was adequate, except the failure to estimate tag loss introduced a positive bias of unknown magnitude. On a perhaps more refined but still subjective level, one could evaluate complementary stratifications of the two-sample data (e.g. recovery rate by application period vs. tag incidence by recovery period) to determine if the observed biases likely biased the population estimate. This approach would not provide particularly useful results in the current study because few of the sampling biases were statistically significant (Fig. 6), and other factors such as stress and the selective loss of tags likely introduced errors that obscured the effect of sampling bias. This approach requires further evaluation and should be developed in a quantitative manner. Ultimately, however, approaches that require the subjective evaluation of data are not useful surrogates for reliable analytic tools. Simulations are required to understand why the MLE is ineffective with this type of data and to develop a functional stratified Petersen estimator.

ARE THE STUDY RESULTS TRANSFERABLE TO OTHER PROJECTS?

This study identifies a number of concerns regarding tag loss, the role of stress, and the utility of stratified population estimators. Given that different field methods are commonly used in other mark-recapture studies in the Fraser River and elsewhere, the question of whether these results are generally transferable needs to be addressed.

An absence of tag loss is one of the principle assumptions underlying the mark-recapture technique. Because the potential for tag loss is always present, it must be assessed in all studies. Similarly, there is evidence of considerable mixing of tags across recovery strata in most

Fraser River sockeye studies (e.g. Schubert 1997; Schubert and Tadey 1997); consequently, the conclusions reached regarding the utility of the MLE and Schaefer estimators are applicable to other sockeye studies. It is the issue of stress and sampling selectivity where the results may be more site-specific. The degree of handling (and presumably stress) was particularly severe in this study because, in addition to capture and tagging, it was necessary to move the fish to a pen where they were held for varying periods. Consequently, the insights into the impact of stress on estimation accuracy may not be transferable to other studies that use less stressful methods. What is transferable is the concept that stress is a potential source of insidious bias. All studies should be designed to minimize stressful handling procedures.

Another unique aspect of this study is that, by tagging at the fence, it should have been possible to apply tags representatively across the population. In fact, the tagging was nonrepresentative, both temporally and by sex. The former can be explained by operational problems; the latter suggests that there are sex-specific difference in the way that fish approach and pass through an enumeration fence that lead to differential vulnerabilities to capture. Because capture techniques can introduce biases that are difficult to anticipate, future studies should evaluate whether beach seining, the capture technique used in most other mark-recapture studies, introduces biases that might reduce the accuracy of population estimates.

CONCLUSIONS

1. The pooled Petersen estimates had errors ranging from -1% to +18% of the true population size. The failure to assess tag loss contributed to the error, but tag loss alone does not fully explain the magnitude of the error.

2. Estimation error results from a lower probability of recovery of tagged versus untagged sockeye. This represents a violation of one of the fundamental assumptions underlying the mark-recapture technique, with different mechanisms affecting each sex. Among males, handling stress may have impaired the ability of tagged fish to migrate further upstream and caused an earlier death. Among females, a combination of factors (tag loss, predator removal, and the failure of technicians to recognize tagged fish) in combination with the effects of subacute stress may have reduced the recoverability of tagged fish. There is a need in future studies to minimize stress and to better assess selective behaviour among predators and technicians.

3. Under conditions of sampling bias, the Schaefer estimator will not substantially improve the accuracy of a PPE estimate, and the exploration of alternate pooling scenarios will not provide useful additional information. The Schaefer estimator should be abandoned for use in population estimation.

4. The ML Darroch estimator can potentially provide estimates that improve the accuracy of the PPE. Currently, there is no obvious way to select among accurate and highly biased ML Darroch estimates. There also is evidence that it will produce biased estimates if there is mixing of tags across recovery strata. The use of the ML Darroch estimator, therefore, should be suspended pending further mathematical development.

5. In the interim, the PPE should be adopted as the sole population estimator, with alternate procedures developed to permit the qualitative and, ultimately, quantitative evaluation of bias.

RECOMMENDATIONS

1. Procedures used to set daily tagging targets should be improved to ensure that tags are applied to each sex at a rate of 1% of each day's migration.

2. The resurvey of carcass recovery areas is an important component of a mark-recapture study because, for a number of reasons, errors can be made in the identification of disk tags during the initial survey. The following changes are recommended to reduce the incidence of missed tags and improve the resurvey component of this study:

- Staff training must emphasize the importance of thoroughly examining each carcass for a tag;
- Crew chiefs should resurvey the recovery areas more frequently, and provide immediate feedback and retraining to crew members

who miss tags;

- The resurvey should begin shortly after the start of the main surveys to make it temporally more representative.

3. Secondary tags or marks should be applied to sockeye released with disk tags to permit the assessment of disk tag loss. In 1995, all disk tagged fish should receive a sex-specific opercular punch as a secondary mark. Implicit in this recommendation is the need for improved staff training and feedback discussed under Recommendation No. 2; improved training and clear standards for what constitutes a releasable tag would also reduce actual tag loss.

4. The stresses that may result from capture, handling and tagging sockeye were identified as a potentially serious source of estimation bias. Fish handling procedures should be modified to ensure that: activity near the fence is minimized; the fish are counted through the fence before large numbers accumulate; holding time in the trap and boxes is minimized; fish are removed from the water for tagging only when a tagger is ready and processed as quickly as possible; when removed from the water, the fish are cradled in two hands rather than dangled by the caudal peduncle; and when released, the fish are gently thrown the minimum necessary distance.

5. With the above modifications, the study will provide a valid comparison of the mark-recapture technique against a known population under the conditions proportional tagging by sex and minimal stress. While such a study will provide useful insights into estimation error, such insights may not be directly transferable to standard mark-recapture studies. Consequently, a second mark-recapture study should be conducted with tags applied to sockeye holding in the river to evaluate the impact of sampling selectivity biases associated with a standard study design.

6. The effect of the visibility of the tag on the probability of recovery by predators or technicians should be investigated by applying clear and red tags to representative portions of the population.

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REFERENCES

Andrew, J.H., and T.M. Webb. MS 1987. Review and assessment of adult sockeye salmon enum-ertion programs on the Fraser River. Prepared by Environmental and Social Systems Analysis Ltd. for the Department of Fisheries and Oceans, New Westminster.

Anon. 1966. Effects of log driving on the salmon and trout populations in the Stellako River. Inter-national Pacific Salmon Fisheries Commission Progress Report No. 14: 88 p.

Arnason, A.N., C.W. Kirby, C.J. Schwarz, and J.R. Irvine. 1996. Computer analysis of data from stratified mark-recovery experiments for estimation of salmon escapements and other populations. Can. Tech. Rep. Fish. Aquat. Sci. 2106: 37 p.

Cutter, R.I., and L.E. Whitesel. 1956. Collection and interpretation of sockeye salmon scales. International Pacific Salmon Fisheries Commission Bulletin 9: 159 p.

Eames, M., T. Quinn, K. Reidinger and D. Haring. 1981. Northern Puget Sound 1976 coho and chum tagging studies. Wash. Dept. Fish. Tech. Rep. No. 64: 217 p.

Environment Canada. 1991. Historic stream flow summary, British Columbia, to 1990. Inland Waters Directorate, Water Resources Branch, Ottawa.

Howard, G.V. 1948. Problems in enumeration of populations of sockeye salmon. Part 1. A study of tagging methods in the enumeration of sockeye salmon populations. International Pacific Salmon Fisheries Commission Bulletin II: 4-66.

Irvine, J.R., J.F.T. Morris, and L.M. Cobb. 1993. Area-under-the-curve salmon escapement estimation manual. Can. Tech. Rep. Fish. Aquat. Sci. 1932: 84 p.

Northcote, T.G., and P.A. Larkin. 1989. The Fraser River: a major salmonine production system, p. 172-204 *In:* D.P. Dodge (ed.) Proceedings of the International Large River Symposium (LARS). Can. Spec. Publ. Fish. Aquat. Sci. 106: 629 p.

Otis, D.L., K.P. Burnham, G.C. White, and D.R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs No. 62: 135 p.

Plante, N. 1990. Estimation de la taille d'une population animale à l'aide d'un modèle de capture-recapture avec stratification. M.Sc. thesis, Université Laval, Quebec

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

Schaefer, M.B. 1951. A study of the spawning populations of sockeye salmon in the Harrison River system, with special reference to the problem of enumeration by means of marked members. International Pacific Salmon Fisheries Commission Bulletin IV: 207p.

Schubert, N.D. 1997. Estimation of the 1994 Mitchell River system sockeye salmon (*Oncorhynchus nerka*) escapement. Can. Manuscr. Rep. Fish. Aquat. Sci. 2429: 33 p.

Schubert, N.D. 1998. The 1994 Fraser River sockeye salmon (*Oncorhynchus nerka*) escapement. Can. Tech. Rep. Fish. Aquat. Sci. 2201: 62 p.

Schubert, N.D., and B.P. Fanos. 1997. Estimation of the 1994 late run sockeye salmon (*Oncorhynchus nerka*) escapement to the Stuart River system. Can. Manuscr. Rep. Fish. Aquat. Sci. 2431: 66 p.

Schubert, N.D., and J.A. Tadey. 1997. Estimation of the 1994 Birkenhead River sockeye salmon (*Oncorhynchus nerka*) escapement. Can. Manuscr. Rep. Fish. Aquat. Sci. 2399: 35 p.

Schwarz, C.J., and C.G. Taylor. 1998. Use of the stratified-Petersen estimator in fisheries ma-nagement: estimating the number of pink salmon (*Oncorhynchus gorbuscha*) spawners in the Fraser River. Can. J. Fish. Aquat. Sci. 55: 281-296.

Seber, G.A.F. 1982. The estimation of animal abundance and related parameters, second edition. Griffin, London.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry, the principles and practices of statistics in biological research, 2nd edition. W.H. Freeman and Co., New York.

Staley, M.J. 1990. Abundance, age, size, sex and coded wire tag recoveries for chinook salmon escapements of the Harrison River, 1984-1988. Can. MS Rep. Fish. Aquat. Sci. 2066: 42 p.

White, G.C., and K.P. Burnham. 1997. Program MARK: survival estimation from populations of marked animals. Colorado State University, Fort Collins. Unpublished draft.

Woodey, J.C. 1984. Escapement estimation in the management of Fraser River sockeye salmon, p. 121-132 *In:* Symons, P.E.K., and M. Waldichuk (eds.) Proceedings of the workshop on stream indexing for salmon escapement estimation, West Vancouver, B.C., 2-3 February 1984. Can. Tech. Rep. Fish. Aquat. Sci. 1326: 258 p.

Appendices

Appendix 1. Annual date of sockeye salmon arrival and peak spawning, jack and adult escapement by sex, percent spawning success and the number of females which had spawned effectively in the Stellako River, 1938-1994.

Year	Arrival	Period of peak spawning	Escapement				Percent spawning success	Effective females
			Total	Jacks	Males	Females		
1938	13-Sep	-	6,943	0	3,124	3,819	91.1%	3,477
1939	15-Sep	-	2,585	0	1,084	1,501	91.1%	1,367
1940	25-Aug	-	3,276	32	1,348	1,896	91.1%	1,726
1941	13-Sep	01-Oct to 05-Oct	8,566	25	3,740	4,801	91.1%	4,371
1942	07-Sep	29-Sep to 02-Oct	91,840	0	32,805	59,035	95.9%	56,626
1943	07-Sep	13-Oct to 18-Oct	14,897	0	5,005	9,892	97.8%	9,674
1944	07-Sep	30-Sep to 06-Oct	5,768	0	2,636	3,132	91.1%	2,852
1945	15-Sep	13-Oct to 18-Oct	20,826	292	8,872	11,662	99.6%	11,617
1946	01-Sep	13-Oct to 18-Oct	245,172	0	92,920	152,252	98.0%	149,207
1947	01-Sep	20-Sep to 28-Sep	59,904	19	30,809	29,076	97.2%	28,268
1948	15-Sep	13-Oct to 18-Oct	16,213	450	6,161	9,602	96.3%	9,242
1949	01-Sep	20-Sep to 28-Sep	104,835	115	44,848	59,872	67.2%	40,231
1950	28-Aug	30-Sep to 01-Oct	145,108	87	58,957	86,064	90.0%	77,410
1951	26-Aug	28-Sep to 01-Oct	96,208	132	41,236	54,840	93.8%	51,413
1952	20-Aug	26-Sep to 30-Sep	40,466	82	19,871	20,513	97.1%	19,920
1953	18-Aug	24-Sep to 26-Sep	43,688	1,554	21,128	21,006	97.1%	20,388
1954	29-Aug	25-Sep to 27-Sep	141,882	23	66,715	75,144	96.2%	72,273
1955	01-Sep	23-Sep to 26-Sep	51,746	7	20,610	31,129	96.2%	29,937
1956	28-Aug	24-Sep to 27-Sep	38,459	21	15,754	22,684	98.2%	21,686
1957	25-Aug	28-Sep to 04-Oct	38,921	399	19,320	19,202	94.0%	18,044
1958	05-Sep	29-Sep to 04-Oct	112,273	22	50,305	61,946	99.4%	61,581
1959	01-Sep	26-Sep to 28-Sep	79,355	50	36,869	42,436	98.7%	41,872
1960	31-Aug	24-Sep to 28-Sep	38,884	4	15,589	23,291	97.5%	22,718
1961	20-Aug	26-Sep to 29-Sep	47,241	378	21,391	25,472	71.2%	18,136
1962	04-Sep	29-Sep to 04-Oct	124,495	10	58,560	65,925	67.6%	44,532
1963	20-Aug	23-Sep to 27-Sep	138,805	11	64,625	74,169	56.0%	41,535
1964	05-Sep	26-Sep to 30-Sep	31,047	157	14,361	16,529	97.9%	16,161
1965	21-Aug	27-Sep to 30-Sep	39,418	33	18,301	21,084	97.1%	20,479
1966	26-Aug	26-Sep to 01-Oct	101,684	155	46,878	54,651	94.3%	51,509
1967	25-Aug	26-Sep to 30-Sep	91,525	45	37,486	53,994	60.1%	32,467
1968	27-Aug	22-Sep to 26-Sep	30,420	52	14,952	15,416	88.7%	13,680
1969	25-Aug	25-Sep to 28-Sep	49,341	130	20,756	28,455	91.5%	25,629
1970	27-Aug	29-Sep to 02-Oct	45,876	79	16,600	29,197	91.5%	26,727
1971	25-Aug	25-Sep to 27-Sep	39,726	35	18,964	20,727	97.2%	20,147
1972	29-Aug	26-Sep to 29-Sep	36,771	71	15,983	20,717	98.4%	19,938
1973	05-Sep	23-Sep to 28-Sep	30,755	351	14,444	15,960	96.6%	15,424
1974	25-Aug	30-Sep to 04-Oct	41,473	198	16,806	24,469	96.9%	23,718
1975	-	29-Sep to 05-Oct	176,079	138	68,381	107,560	63.6%	68,451
1976	-	29-Sep to 03-Oct	150,741	7	76,158	74,576	87.6%	63,865
1977	08-Sep	23-Sep to 29-Sep	23,452	405	10,708	12,339	88.3%	10,894
1978	01-Sep	24-Sep to 30-Sep	60,421	1,523	25,498	33,400	97.4%	32,528
1979	-	28-Sep to 03-Oct	290,116	74	125,904	164,138	93.0%	152,583
1980	-	24-Sep to 28-Sep	72,073	23	32,907	39,143	72.8%	28,477
1981	-	29-Sep to 04-Oct	22,021	195	9,331	12,495	96.3%	12,030
1982	-	25-Sep to 30-Sep	69,434	14	30,946	38,474	90.7%	34,888
1983	-	20-Sep to 25-Sep	121,739	47	54,920	66,772	91.9%	61,357
1984	-	20-Sep to 25-Sep	60,973	16	27,594	33,363	97.9%	32,672
1985	-	23-Sep to 28-Sep	42,296	197	19,064	23,035	95.4%	21,969

[a] Includes fish removed for sampling.

Continued

Appendix 1. Annual date of sockeye salmon arrival and peak spawning, jack and adult escapement by sex, percent spawning success and the number of females which had spawned effectively in the Stellako River, 1938-1994, continued.

Year	Arrival	Period of peak spawning	Escapement				Percent spawning success	Effective females
			Total	Jacks	Males	Females		
1986	-	29-Sep to 03-Oct	77,378	201	31,234	45,943	97.1%	44,564
1987	-	29-Sep to 03-Oct	211,111	26	98,430	112,655	87.2%	98,179
1988	-	25-Sep to 30-Sep	367,751	49	146,574	221,128	90.7%	200,537
1989	-	27-Sep to 04-Oct	43,189	10	25,458	17,721	89.9%	15,903
1990	-	25-Sep to 02-Oct	93,928	8	37,043	56,877	99.4%	56,537
1991	-	-	94,931	47	40,205	54,679	99.5%	54,348
1992	-	-	97,985	6	42,478	55,501	99.4%	55,138
1993	-	25-Sep to 01-Oct	91,443	372	46,525	44,546	96.3%	42,859
1994	Late Aug	15-Sep to 25-Sep	142,092	145	68,609	73,338	90.0%	66,019

Appendix 2. Live and dead sockeye counts, by date and survey method, in the Stellako River, 1994.

River	Location	Date	Survey method	Sockeye counts	
				Live	Dead
Stellako River	Above fence	31-Aug	Boat	7,250	0
Stellako River	Below fence	28-Sep	Boat	5,000	n/r
		4-Oct	Boat	2,200	n/r
		8-Oct	Boat	1,100	n/r
		12-Oct	Boat	300	n/r

Appendix 3. Daily counts of live sockeye salmon, native fishery harvest, and the daily application of disk tags by sex (field estimate and correction for sex identification error), at the Stellako River enumeration fence, 1994.

			Disk tag application								
			Original field estimate of sex composition				Corrected for sex identification error[c]				
Date	Live count[a]	Native fishery harvest[b]	Male	Female	Jack	Total	Male	Female	Jack	Total	Percent tagged
31-Aug	895	0	4	15	0	19	4 [d]	15 [d]	0	19	2.1%
1-Sep	110	0	10	9	2	21	10 [d]	9	2	21	19.1%
2-Sep	305	0	18	19	1	38	18	19 [d]	1	38	12.5%
3-Sep	692	0	0	0	0	0	0	0	0	0	0.0%
4-Sep	2,192	0	7	14	1	22	7	14	1	22	1.0%
5-Sep	1,100	42	5	12	0	17	5	12	0	17	1.5%
6-Sep	17,340	56	16	29	3	48	15	30	3	48	0.3%
7-Sep	6,384	40	6	4	0	10	6	4	0	10	0.2%
8-Sep	5,266	50	28	96	1	125	26	98	1	125	2.4%
9-Sep	8,138	67	0	0	0	0	0	0	0	0	0.0%
10-Sep	6,434	59	25	55	1	81	24	56	1	81	1.3%
11-Sep	6,209	84	23	95	1	119	21	97 [d]	1	119	1.9%
12-Sep	6,527	61	5	30	1	36	4	31	1	36	0.6%
13-Sep	8,311	93	16	57	2	75	15	58	2	75	0.9%
14-Sep	4,360	121	11	28	0	39	10	29	0	39	0.9%
15-Sep	7,169	70	20	28	2	50	19	29	2	50	0.7%
16-Sep	5,570	77	18	82	0	100	17	83 [d]	0	100	1.8%
17-Sep	5,271	101	26	72	2	100	25	73 [d]	2	100	1.9%
18-Sep	4,260	78	1	7	0	8	1	7 [d]	0	8	0.2%
19-Sep	3,628	40	6	48	0	54	5 [d]	49	0	54	1.5%
20-Sep	1,162	50	22	16	0	38	22	16	0	38	3.3%
21-Sep	2,625	0	23	38	1	62	22 [d]	39 [e]	1	62	2.4%
22-Sep	2,953	26	5	11	0	16	5	11	0	16	0.5%
23-Sep	3,302	32	24	23	0	47	24	23	0	47	1.4%
24-Sep	3,185	0	5	15	1	21	5	15 [f]	1	21	0.7%
25-Sep	1,444	0	0	0	0	0	0	0	0	0	0.0%
26-Sep	1,076	0	8	13	0	21	8 [d]	13 [d]	0	21	2.0%
27-Sep	1,250	0	0	10	0	10	0	10	0	10	0.8%
28-Sep	665	0	0	0	0	0	0	0	0	0	0.0%
29-Sep	242	0	0	0	0	0	0	0	0	0	0.0%
30-Sep	1,087	0	0	0	0	0	0	0	0	0	0.0%
1-Oct	1,107	0	11	36	1	48	10	37	1	48	4.3%
2-Oct	418	0	0	0	0	0	0	0	0	0	0.0%
3-Oct	413	0	0	0	0	0	0	0	0	0	0.0%
4-Oct	73	0	0	0	0	0	0	0	0	0	0.0%
5-Oct	52	0	0	0	0	0	0	0	0	0	0.0%
6-Oct	132	0	0	0	0	0	0	0	0	0	0.0%
7-Oct	77	0	0	0	0	0	0	0	0	0	0.0%
8-Oct	81	0	0	0	0	0	0	0	0	0	0.0%
9-Oct	16	0	0	0	0	0	0	0	0	0	0.0%
10-Oct	3	0	0	0	0	0	0	0	0	0	0.0%
11-Oct	1	0	0	0	0	0	0	0	0	0	0.0%
12-Oct	0	0	0	0	0	0	0	0	0	0	-
Total	121,525	1,147	343	862	20	1,225	328	877	20	1,225	1.01%

[a] Includes adults and jacks, and sockeye released untagged and with disk tags.

[b] Not included in live count; includes fecundity samples.

[c] See methods for sex identification error correction procedures.

[d] Includes 1 recovered on the enumeration fence less than 5-days after release.

[e] Includes 2 recovered on the enumeration fence less than 5-days after release.

[f] Includes 1 recovered on the spawning grounds and 1 on the enumeration fence less than 5-days after release.

Appendix 4a. Incidence of net, lamprey and hook marks and of *Flexibacter columnaris* lesions among adult male sockeye examined at tag application at the Stellako River enumeration fence, 1994. [a]

Date	Number of adult males examined	Net marks		Lamprey marks		Hook marks		*F. columnaris* [b]	
		Number	Percent	Number	Percent	Number	Percent	Number	Percent
31-Aug	4	0	0.0%	0	0.0%	0	0.0%	0	0.0%
1-Sep	10	0	0.0%	0	0.0%	0	0.0%	0	0.0%
2-Sep	18	3	16.7%	0	0.0%	0	0.0%	0	0.0%
3-Sep	0	0	-	0	-	0	-	0	-
4-Sep	7	1	14.3%	0	0.0%	0	0.0%	0	0.0%
5-Sep	5	1	20.0%	0	0.0%	0	0.0%	0	0.0%
6-Sep	16	2	12.5%	0	0.0%	0	0.0%	0	0.0%
7-Sep	6	1	16.7%	0	0.0%	0	0.0%	0	0.0%
8-Sep	28	5	17.9%	0	0.0%	0	0.0%	0	0.0%
9-Sep	0	0	-	0	-	0	-	0	-
10-Sep	25	11	44.0%	0	0.0%	0	0.0%	0	0.0%
11-Sep	23	7	30.4%	0	0.0%	0	0.0%	0	0.0%
12-Sep	5	1	20.0%	0	0.0%	0	0.0%	0	0.0%
13-Sep	16	3	18.8%	0	0.0%	1	6.3%	0	0.0%
14-Sep	11	2	18.2%	0	0.0%	0	0.0%	0	0.0%
15-Sep	20	7	35.0%	0	0.0%	0	0.0%	0	0.0%
16-Sep	18	9	50.0%	0	0.0%	0	0.0%	0	0.0%
17-Sep	26	6	23.1%	0	0.0%	0	0.0%	0	0.0%
18-Sep	1	0	0.0%	0	0.0%	1	100.0%	0	0.0%
19-Sep	6	3	50.0%	0	0.0%	0	0.0%	0	0.0%
20-Sep	22	4	18.2%	0	0.0%	0	0.0%	0	0.0%
21-Sep	23	4	17.4%	0	0.0%	0	0.0%	0	0.0%
22-Sep	5	2	40.0%	0	0.0%	0	0.0%	0	0.0%
23-Sep	24	0	0.0%	0	0.0%	0	0.0%	0	0.0%
24-Sep	5	0	0.0%	0	0.0%	0	0.0%	0	0.0%
25-Sep	0	0	-	0	-	0	-	0	-
26-Sep	8	4	50.0%	0	0.0%	0	0.0%	0	0.0%
27-Sep	0	0	-	0	-	0	-	0	-
28-Sep	0	0	-	0	-	0	-	0	-
29-Sep	0	0	-	0	-	0	-	0	-
30-Sep	0	0	-	0	-	0	-	0	-
1-Oct	11	4	36.4%	0	0.0%	0	0.0%	0	0.0%
Total	343	80	23.3%	0	0.0%	2	0.6%	0	0.0%

[a] Not corrected for sex identification error; includes tagged sockeye removed from the application sample (Appendix 3).

[b] Not assessed in 1994.

Appendix 4b. Incidence of net, lamprey and hook marks and of *Flexibacter columnaris* lesions among female sockeye examined at tag application at the Stellako River enumeration fence, 1994. [a]

Date	Number of females examined	Net marks		Lamprey marks		Hook marks		*F. columnaris* [b]	
		Number	Percent	Number	Percent	Number	Percent	Number	Percent
31-Aug	15	1	6.7%	0	0.0%	0	0.0%	0	0.0%
1-Sep	9	2	22.2%	0	0.0%	0	0.0%	0	0.0%
2-Sep	19	8	42.1%	0	0.0%	0	0.0%	0	0.0%
3-Sep	0	0	-	0	-	0	-	0	-
4-Sep	14	3	21.4%	0	0.0%	0	0.0%	0	0.0%
5-Sep	12	6	50.0%	0	0.0%	0	0.0%	0	0.0%
6-Sep	29	7	24.1%	0	0.0%	0	0.0%	0	0.0%
7-Sep	4	1	25.0%	0	0.0%	0	0.0%	0	0.0%
8-Sep	96	15	15.6%	0	0.0%	0	0.0%	0	0.0%
9-Sep	0	0	-	0	-	0	-	0	-
10-Sep	55	16	29.1%	0	0.0%	0	0.0%	0	0.0%
11-Sep	95	27	28.4%	0	0.0%	0	0.0%	0	0.0%
12-Sep	30	7	23.3%	0	0.0%	0	0.0%	0	0.0%
13-Sep	57	17	29.8%	0	0.0%	0	0.0%	0	0.0%
14-Sep	28	13	46.4%	0	0.0%	0	0.0%	0	0.0%
15-Sep	28	16	57.1%	0	0.0%	0	0.0%	0	0.0%
16-Sep	82	30	36.6%	0	0.0%	0	0.0%	0	0.0%
17-Sep	72	27	37.5%	0	0.0%	0	0.0%	0	0.0%
18-Sep	7	1	14.3%	0	0.0%	0	0.0%	0	0.0%
19-Sep	48	25	52.1%	0	0.0%	0	0.0%	0	0.0%
20-Sep	16	1	6.3%	0	0.0%	0	0.0%	0	0.0%
21-Sep	38	13	34.2%	0	0.0%	0	0.0%	0	0.0%
22-Sep	11	4	36.4%	0	0.0%	0	0.0%	0	0.0%
23-Sep	23	0	0.0%	0	0.0%	0	0.0%	0	0.0%
24-Sep	15	1	6.7%	0	0.0%	0	0.0%	0	0.0%
25-Sep	0	0	-	0	-	0	-	0	-
26-Sep	13	6	46.2%	0	0.0%	0	0.0%	0	0.0%
27-Sep	10	2	20.0%	0	0.0%	0	0.0%	0	0.0%
28-Sep	0	0	-	0	-	0	-	0	-
29-Sep	0	0	-	0	-	0	-	0	-
30-Sep	0	0	-	0	-	0	-	0	-
1-Oct	36	11	30.6%	0	0.0%	0	0.0%	0	0.0%
Total	862	260	30.2%	0	0.0%	0	0.0%	0	0.0%

[a] Not corrected for sex identification error; includes tagged sockeye removed from the application sample (Appendix 3).

[b] Not assessed in 1994.

Appendix 4c. Incidence of net, lamprey and hook marks and of *Flexibacter columnaris* lesions among jack sockeye examined at tag application at the Stellako River enumeration fence, 1994.

Date	Number of jacks examined	Net marks		Lamprey marks		Hook marks		*F. columnaris* [a]	
		Number	Percent	Number	Percent	Number	Percent	Number	Percent
31-Aug	0	0	-	0	-	0	-	0	-
1-Sep	2	0	0.0%	0	0.0%	0	0.0%	0	0.0%
2-Sep	1	0	0.0%	0	0.0%	0	0.0%	0	0.0%
3-Sep	0	0	-	0	-	0	-	0	-
4-Sep	1	0	0.0%	0	0.0%	0	0.0%	0	0.0%
5-Sep	0	0	-	0	-	0	-	0	-
6-Sep	3	0	0.0%	0	0.0%	0	0.0%	0	0.0%
7-Sep	0	0	-	0	-	0	-	0	-
8-Sep	1	0	0.0%	0	0.0%	0	0.0%	0	0.0%
9-Sep	0	0	-	0	-	0	-	0	-
10-Sep	1	1	100.0%	0	0.0%	0	0.0%	0	0.0%
11-Sep	1	0	0.0%	0	0.0%	0	0.0%	0	0.0%
12-Sep	1	0	0.0%	0	0.0%	0	0.0%	0	0.0%
13-Sep	2	0	0.0%	0	0.0%	0	0.0%	0	0.0%
14-Sep	0	0	-	0	-	0	-	0	-
15-Sep	2	0	0.0%	0	0.0%	0	0.0%	0	0.0%
16-Sep	0	0	-	0	-	0	-	0	-
17-Sep	2	2	100.0%	0	0.0%	0	0.0%	0	0.0%
18-Sep	0	0	-	0	-	0	-	0	-
19-Sep	0	0	-	0	-	0	-	0	-
20-Sep	0	0	-	0	-	0	-	0	-
21-Sep	1	0	0.0%	0	0.0%	0	0.0%	0	0.0%
22-Sep	0	0	-	0	-	0	-	0	-
23-Sep	0	0	-	0	-	0	-	0	-
24-Sep	1	0	0.0%	0	0.0%	0	0.0%	0	0.0%
25-Sep	0	0	-	0	-	0	-	0	-
26-Sep	0	0	-	0	-	0	-	0	-
27-Sep	0	0	-	0	-	0	-	0	-
28-Sep	0	0	-	0	-	0	-	0	-
29-Sep	0	0	-	0	-	0	-	0	-
30-Sep	0	0	-	0	-	0	-	0	-
1-Oct	1	0	0.0%	0	0.0%	0	0.0%	0	0.0%
Total	20	3	15.0%	0	0.0%	0	0.0%	0	0.0%

[a] Not assessed in 1994.

Appendix 5. Daily number of sockeye carcasses, by location, mark status and sex, recovered on the Stellako River spawning grounds, 1994.

Date	Area	Number of surveys	Disk tag present			Untagged			Total		
			Male	Female	Jack	Male	Female	Jack	Male	Female	Jack
26-Sep	1	-	0	2	0	67	123	0	67	125	0
	2	-	0	0	0	30	92	0	30	92	0
	3	-	0	0	0	57	102	0	57	102	0
	4	-	1	2	0	113	177	1	114	179	1
	5	-	0	0	0	56	74	0	56	74	0
	6	-	0	2	0	53	75	0	53	77	0
27-Sep	7	-	0	7	0	189	261	2	189	268	2
	8	-	1	1	0	224	274	0	225	275	0
	9	-	8	16 [b]	1	1,257	1,341	0	1,265	1,357	1
28-Sep	1	-	1	2	0	103	166	0	104	168	0
	2	-	0	0	0	76	122	0	76	122	0
	3	-	0	1	0	58	113	0	58	114	0
	4	-	2	3	0	130	223	0	132	226	0
	5	-	2	0	0	76	85	1	78	85	1
	6	-	0	3	0	68	92	1	68	95	1
	9[a]	-	2	3	0	144	120	0	146	123	0
29-Sep	7	-	5	7	0	367	476	2	372	483	2
	8	-	1	2	0	270	298	2	271	300	2
	9[a]	-	3	11	1	1,506	1,395	4	1,509	1,406	5
30-Sep	1	-	1	0	0	274	421	0	275	421	0
	2	-	1	3	0	118	186	0	119	189	0
	3	-	3	3	0	157	310	1	160	313	1
	4	-	1	6	0	196	315	1	197	321	1
	5	-	1	2	0	179	156	0	180	158	0
	6	-	0	0	0	148	186	1	148	186	1
	9[a]	-	3	0	0	42	39	0	45	39	0
1-Oct	7	-	3	3	0	416	487	1	419	490	1
	8	-	1	5	0	320	336	1	321	341	1
	9[a]	-	1	7	0	1,134	813	0	1,135	820	0
2-Oct	1	-	0	4	0	283	321	0	283	325	0
	2	-	1	2	0	148	175	0	149	177	0
	3	-	0	5	1	144	334	0	144	339	1
	4	-	2	2	0	240	279	1	242	281	1
	5	-	0	0	0	215	203	0	215	203	0
	6	-	1	2	1	163	186	0	164	188	1
3-Oct	7	-	1	7	0	337	499	0	338	506	0
	8	-	0	3	0	261	292	0	261	295	0
	9	-	5	13	0	1,060	1,078	0	1,065	1,091	0
6-Oct	1	-	2	6	0	752	862	3	754	868	3
	2	-	0	4	0	469	606	1	469	610	1
	3	-	2	10	0	769	1,021	2	771	1,031	2
	4	-	2	13	0	553	762	1	555	775	1
	5	-	2	5	1	383	484	1	385	489	2
	6	-	2	7	1	267	289	0	269	296	1
7-Oct	7	-	4	7	0	540	727	1	544	734	1
	8	-	2	5	0	275	534	3	277	539	3
	9	-	4	12	0	1,174	1,318	1	1,178	1,330	1
8-Oct	1	-	1	3	0	310	399	0	311	402	0
	2	-	0	2	0	250	322	0	250	324	0
	3	-	1	5	0	255	439	0	256	444	0
	4	-	1	3	0	232	420	1	233	423	1
	5	-	0	3	0	168	222	0	168	225	0

Continued

Appendix 5. Daily number of sockeye carcasses, by location, mark status and sex, recovered on the Stellako River spawning grounds, 1994 continued.

Date	Area	Number of surveys	Disk tag present			Untagged			Total		
			Male	Female	Jack	Male	Female	Jack	Male	Female	Jack
8-Oct	6	-	0	1	0	355	374	0	355	375	0
9-Oct	7	-	1	2	0	261	273	1	262	275	1
	8	-	0	2	0	174	271	0	174	273	0
	9	-	5	5	0	436	654	0	441	659	0
10-Oct	1	-	1	5	0	243	372	1	244	377	1
	2	-	0	2	0	173	265	0	173	267	0
	3	-	0	3	0	269	379	1	269	382	1
	4	-	1	5	0	323	447	0	324	452	0
	5	-	2	1	0	142	169	0	144	170	0
	6	-	2	2	0	190	179	0	192	181	0
11-Oct	7	-	0	1	0	175	327	0	175	328	0
	8	-	0	0	0	82	182	0	82	182	0
	9	-	1	3	0	298	508	1	299	511	1
12-Oct	1	-	0	1	0	157	273	0	157	274	0
	2	-	0	5	0	208	346	0	208	351	0
	3	-	0	1	0	196	331	1	196	332	1
	4	-	0	1	0	142	300	0	142	301	0
	5	-	0	2	0	163	183	2	163	185	2
	6	-	0	1	0	158	192	0	158	193	0
13-Oct	7	-	1	2	0	136	223	0	137	225	0
	8	-	0	1	0	34	88	0	34	89	0
	9	-	0	0	0	20	60	0	20	60	0
15-Oct	1	-	0	5	0	136	221	0	136	226	0
	2	-	0	2	0	63	135	0	63	137	0
	3	-	0	3	0	164	271	0	164	274	0
	4	-	0	4	1	228	327	0	228	331	1
	5	-	0	1	0	141	156	1	141	157	1
	6	-	0	0	0	108	156	0	108	156	0
16-Oct	7	-	0	0	0	18	40	0	18	40	0
	8	-	0	0	0	22	79	0	22	79	0
	9	-	1	3	0	184	447	0	185	450	0
17-Oct	1	-	0	1	0	44	88	1	44	89	1
	2	-	0	0	0	78	108	0	78	108	0
	3	-	0	0	0	37	85	1	37	85	1
	4	-	0	1	0	51	126	0	51	127	0
	5	-	0	1	0	45	63	1	45	64	1
	6	-	0	1	0	59	95	0	59	96	0
	9	-	0	0	0	22	0	0	22	0	0
Total	1	10	6	29	0	2,369	3,246	5	2,375	3,275	5
	2	10	2	20	0	1,613	2,357	1	1,615	2,377	1
	3	10	6	31	1	2,106	3,385	6	2,112	3,416	7
	4	10	10	40	1	2,208	3,376	5	2,218	3,416	6
	5	10	7	15	1	1,568	1,795	6	1,575	1,810	7
	6	10	5	19	2	1,569	1,824	2	1,574	1,843	4
	7	9	15	36	0	2,439	3,313	7	2,454	3,349	7
	8	9	5	19	0	1,662	2,354	6	1,667	2,373	6
	9	12	33	73	2	7,277	7,773	6	7,310	7,846	8
	Total	-	89	282	7	22,811	29,423	44	22,900	29,705	51

[a] Partial survey.

[b] One disk tag was excluded because elapsed time between release and recovery was less than five days.

Appendix 6. Daily number of sockeye carcasses, by mark status and sex, recovered on the Stellako River enumeration fence, 1994.

	Disk tag present			Untagged			Total		
Date	Male	Female	Jack	Male	Female	Jack	Male	Female	Jack
1-Sep	0	0 [a]	0	0	0	0	0	0 [a]	0
3-Sep	0 [b]	0	0	1	3	0	1 [b]	3	0
4-Sep	0	0 [a]	0	0	1	0	0	1 [a]	0
5-Sep	0	0	0	3	8	0	3	8	0
6-Sep	0	0	0	3	4	0	3	4	0
7-Sep	0	0	0	6	9	0	6	9	0
8-Sep	0	0	0	9	15	0	9	15	0
9-Sep	0	0	0	11	16	0	11	16	0
10-Sep	0	0	0	7	8	0	7	8	0
11-Sep	0	0	0	8	12	0	8	12	0
12-Sep	0	0 [a]	0	10	14	0	10	14 [a]	0
13-Sep	0	0	0	9	17	0	9	17	0
14-Sep	0	1	0	13	19	0	13	20	0
15-Sep	0	1	0	13	22	0	13	23	0
16-Sep	0	0	0	16	44	1	16	44	1
17-Sep	0	0	0	20	47	0	20	47	0
18-Sep	0	0	0	18	88	0	18	88	0
19-Sep	0	1	0	25	68	0	25	69	0
20-Sep	0	1 [b]	0	31	103	0	31	104 [b]	0
21-Sep	0	2 [a]	0	72	123	0	72	125 [a]	0
22-Sep	0 [a]	4 [a]	0	102	196	0	102 [a]	200 [a]	0
23-Sep	3	1	0	138	212	4	141	213	4
24-Sep	2 [a]	0	0	235	267	2	237 [a]	267	2
25-Sep	4	2 [a]	0	467	383	0	471	385 [a]	0
26-Sep	2 [a]	1 [a]	0	531	321	0	533 [a]	322 [a]	0
27-Sep	6	3 [a]	1	1,042	722	2	1,048	725 [a]	3
28-Sep	5	4	0	1,290	591	3	1,295	595	3
29-Sep	11	4	0	1,325	529	1	1,336	533	1
30-Sep	9	6	1	1,368	652	3	1,377	658	4
1-Oct	14	17	0	1,605	863	3	1,619	880	3
2-Oct	14	13	0	1,288	657	0	1,302	670	0
3-Oct	4	4	0	1,286	718	3	1,290	722	3
4-Oct	12	12	0	1,416	961	2	1,428	973	2
5-Oct	2	11	0	1,043	880	1	1,045	891	1
6-Oct	2	5	0	804	855	1	806	860	1
7-Oct	1	7	0	634	715	1	635	722	1
8-Oct	2	3	1	604	733	5	606	736	6
9-Oct	7	9	0	681	853	5	688	862	5
10-Oct	0	1	0	385	534	0	385	535	0
11-Oct	1	3	0	238	373	1	239	376	1
12-Oct	0	0	0	84	145	1	84	145	1
Total	101	116	3	16,841	12,781	39	16,942	12,897	42

[a] Excludes 1 disk tag recovered less than 5-days after release.

[b] Excludes 2 disk tags recovered less than 5-days after release.

Appendix 7. Daily number of sockeye carcasses reexamined and disk tags recovered, by location and sex, during the re-survey of the Stellako River, 1994. [a]

Date	Location	Number of surveys	Disk tag present			Total examined			Disk tag incidence		
			Male	Female	Jack	Male	Female	Jack	Male	Female	Jack
4-Oct	1	-	0	1	0	303	310	0	0.000	0.003	-
	2	-	1	2	0	198	239	1	0.005	0.008	0.000
	3	-	0	1	0	167	252	1	0.000	0.004	0.000
	4	-	0	0	0	319	399	0	0.000	0.000	-
	5	-	0	2	0	270	251	1	0.000	0.008	0.000
	6	-	0	0	0	150	131	0	0.000	0.000	-
5-Oct	7	-	0	1	0	248	288	2	0.000	0.003	0.000
	8	-	0	2	0	480	502	0	0.000	0.004	-
	9	-	0	2	0	2,170	2,107	1	0.000	0.001	0.000
10-Oct	7	-	0	1	0	675	865	0	0.000	0.001	-
	8	-	0	3	0	295	545	0	0.000	0.006	-
	9	-	0	0	0	750	870	0	0.000	0.000	-
11-Oct	1	-	1	2	0	426	587	0	0.002	0.003	-
	2	-	1	2	0	408	535	0	0.002	0.004	-
	3	-	0	2	0	336	550	0	0.000	0.004	-
	4	-	0	2	0	500	666	1	0.000	0.003	0.000
	5	-	1	0	0	337	327	1	0.003	0.000	0.000
14-Oct	7	-	0	1	0	300	366	1	0.000	0.003	0.000
	8	-	0	0	0	421	753	0	0.000	0.000	-
	9	-	0	1	0	792	1,099	1	0.000	0.001	0.000
15-Oct	1	-	0	0	0	271	371	4	0.000	0.000	0.000
	2	-	0	0	0	116	150	0	0.000	0.000	-
	3	-	0	1	0	178	324	0	0.000	0.003	-
	4	-	0	0	0	161	254	0	0.000	0.000	-
	5	-	0	0	0	150	210	0	0.000	0.000	-
	6	-	0	0	0	114	159	0	0.000	0.000	-
17-Oct	1	-	0	0	0	7	19	0	0.000	0.000	-
	2	-	0	0	0	9	15	0	0.000	0.000	-
	3	-	0	0	0	14	27	0	0.000	0.000	-
	4	-	0	0	0	34	46	0	0.000	0.000	-
	5	-	0	0	0	23	18	0	0.000	0.000	-
	6	-	0	0	0	25	32	0	0.000	0.000	-
	7	-	0	0	0	71	82	0	0.000	0.000	-
	8	-	0	0	0	54	110	0	0.000	0.000	-
	9	-	0	0	0	74	142	0	0.000	0.000	-
Total	1	4	1	3	0	1,007	1,287	4	0.001	0.002	0.000
	2	4	2	4	0	731	939	1	0.003	0.004	0.000
	3	4	0	4	0	695	1,153	1	0.000	0.003	0.000
	4	4	0	2	0	1,014	1,365	1	0.000	0.001	0.000
	5	4	1	2	0	780	806	2	0.001	0.002	0.000
	6	3	0	0	0	289	322	0	0.000	0.000	-
	7	4	0	3	0	1,294	1,601	3	0.000	0.002	0.000
	8	4	0	5	0	1,250	1,910	0	0.000	0.003	-
	9	4	0	3	0	3,786	4,218	2	0.000	0.001	0.000
	Total	-	4	26	0	10,846	13,601	14	0.0004	0.0019	0.0000

[a] Location codes:

Appendix 8. Fecundity sampling results and analytic details for sockeye salmon sampled at the Stellako River enumeration fence, 1994.

Sample number	Age	Standard length (cm)	Skein weight (g)	Skein sub-sample		Estimated fecundity	Actual fecundity	Misc. eggs	Adjusted fecundity
				Weight (g)	Egg count				
1	4_2	50.3	244.1	114.4	1,449	3,092	3,074	0	3,074
2	4_2	52.7	218.3	102.8	1,501	3,187		0	3,187
3	4_2	50.1	195.3	102.9	1,273	2,416		3	2,419
4	4_2	53.0	224.5	102.5	1,269	2,779		0	2,779
5	4_2	47.6	179.9	114.5	1,527	2,399	2,422	3	2,425
6	4_2	50.5	148.5	102.2	1,837	2,669		0	2,669
7	4_2	47.1	168.1	105.2	1,554	2,483		0	2,483
8	4_2	51.8	190.8	110.0	2,148	3,726		8	3,734
9	4_2	54.2	275.5	123.3	1,878	4,196		6	4,202
10	4_2	50.7	259.2	150.0	1,915	3,309	3,318	0	3,318
11	4_2	53.9	256.1	123.8	1,807	3,738		4	3,742
12	4_2	50.5	184.8	102.6	1,448	2,608		12	2,620
13	4_2	47.3	185.3	102.7	1,628	2,937		1	2,938
14	4_2	50.0	201.1	101.5	1,604	3,178		14	3,192
15	4_2	46.6	142.0	111.3	1,579	2,015	2,004	24	2,028
16	4_2	50.0	205.4	102.5	1,443	2,892		11	2,903
17	4_2	53.1	226.1	103.3	1,400	3,064		17	3,081
18	4_2	51.4	201.9	102.6	1,557	3,064		20	3,084
19	4_2	53.1	184.9	102.4	1,475	2,663		11	2,674
20	4_2	50.0	221.0	145.4	1,900	2,888	2,908	27	2,935
21	4_2	50.0	176.3	101.8	1,616	2,799		14	2,813
22	4_2	54.1	260.7	121.4	1,627	3,494		16	3,510
23	4_2	53.7	181.4	102.3	1,691	2,999		29	3,028
24	4_2	49.4	147.7	101.0	1,655	2,420		40	2,460
25	4_2	51.1	225.8	128.8	2,193	3,845	3,874	3	3,877
26	4_2	50.3	183.0	110.4	1,591	2,637		7	2,644
27	4_2	50.6	214.9	105.5	1,506	3,068		1	3,069
28	4_2	50.1	209.9	102.1	1,132	2,327		2	2,329
29	4_2	51.7	255.7	123.3	1,554	3,223		24	3,247
30	4_2	50.5	205.2	100.7	1,503	3,063	3,075	18	3,093
31	4_2	53.2	210.5	110.5	1,476	2,812		6	2,818
32	4_2	53.0	232.8	103.1	1,409	3,182		0	3,182
33	4_2	51.9	266.6	123.5	1,617	3,491		3	3,494
34	4_2	47.8	175.5	102.8	1,452	2,479		2	2,481
35	4_2	49.4	177.5	120.6	1,899	2,795	2,791	8	2,799
36	4_2	53.2	227.0	122.3	1,557	2,890		0	2,890
37	4_2	54.2	286.6	123.1	1,746	4,065		1	4,066
38	4_2	51.9	244.8	121.4	1,634	3,295		0	3,295
39	4_2	52.3	213.6	104.9	1,305	2,657		3	2,660
40	4_2	53.6	239.4	111.8	1,618	3,465	3,437	0	3,437
41	4_2	56.2	316.1	135.3	1,654	3,864		1	3,865
42	4_2	50.2	193.5	106.5	1,589	2,887		3	2,890
43	4_2	49.4	241.3	121.3	1,666	3,314		5	3,319
44	4_2	51.9	268.8	153.7	1,994	3,487	3,500	4	3,504
45	4_2	49.6	216.7	102.3	1,494	3,165		0	3,165
46	4_2	49.2	177.5	102.1	1,608	2,795		0	2,795
47	4_2	54.0	263.1	124.1	2,034	4,312		8	4,320
48	4_2	52.4	267.3	124.3	1,524	3,277		4	3,281
49	5_2	55.8	243.9	122.3	1,819	3,628		6	3,634
50	5_2	57.5	349.0	143.5	1,939	4,716		2	4,718
Mean	4_2	51.2	216.5	113.3	1,615	3,071	3,040	8	3,080
	5_2	56.7	296.5	132.9	1,879	4,172	-	4	4,176

Appendix 9. Proportion at age and mean length (Standard and POH) at age, by location, sex and sample period, from the adult and jack samples of sockeye carcasses recovered on the Stellako River spawning grounds, 1994. [a]

						Standard length (cm)		POH length (cm)	
Sample type	Sex	Sampling Date	Age	Sample size	Percent	Mean	Standard deviation	Mean	Standard deviation
Adult	Male		5_2	8	14.3%	57.3	3.10	49.6	2.62
			4_2	48	85.7%	53.4	2.26	48.2	1.95
			Unaged	1	-				
			5_2	4	6.7%	57.9	2.00	49.8	1.74
			4_2	56	93.3%	51.5	2.20	44.8	1.83
			Unaged	0	-				
			5_2	5	12.2%	55.1	1.95	48.1	1.87
			4_2	36	87.8%	53.3	2.26	43.3	1.96
			Unaged	1	-				
		Total	5_2	17	10.8%	56.8	2.69	49.2	2.32
			4_2	140	89.2%	52.6	2.39	45.7	2.02
			Unaged	2	-				
	Female		5_2	3	5.2%	55.3	2.01	49.7	1.50
			4_2	55	94.8%	50.4	2.42	45.5	2.01
			Unaged	2	-				
			5_2	7	12.1%	54.9	2.08	49.2	2.03
			4_2	51	87.9%	49.9	2.26	45.0	1.97
			Unaged	2	-				
			5_2	7	12.1%	55.8	1.64	50.3	1.18
			4_2	51	87.9%	50.0	1.75	45.2	1.59
			Unaged	2	-				
		Total	5_2	17	9.8%	55.3	1.82	49.7	1.63
			4_2	157	90.2%	50.1	2.16	45.2	1.93
			Unaged	6	-				
Jack	Both	Total	3_2	4	6.8%	44.9	2.16	-	-
			4_2	55	93.2%	39.4	1.33	36.3	1.21
			Unaged	10	-				

[a] Mean lengths and standard deviations were calculated from length data rounded to the nearest centimeter.

Appendix 10a. Incidence of disk tags in sockeye salmon recovered on the Stellako River spawning grounds, by recovery period and sex, 1994.

Recovery period	Number of surveys	Carcasses recovered with disk tags			Total recovery			Disk tag incidence		
		Male	Female[a]	Jack	Male	Female	Jack	Male	Female	Jack
Similar Recovery Periods										
01-Sep to 22-Sep[b]	0.0	0	0	0	0	0	0	-	-	-
23-Sep to 27-Sep	1.0	10	30	1	2,056	2,549	4	0.5%	1.2%	25.0%
28-Sep to 02-Oct	2.8	35	76	3	7,010	7,913	19	0.5%	1.0%	15.8%
03-Oct to 07-Oct	1.2	26	92	2	6,866	8,564	15	0.4%	1.1%	13.3%
08-Oct to 12-Oct	2.8	16	59	0	5,376	7,886	8	0.3%	0.7%	0.0%
13-Oct to 17-Oct	2.2	2	25	1	1,592	2,793	5	0.1%	0.9%	20.0%
Chi-Square Test Result:								*6.74*	*6.32*	*1.94*
Critical Chi-Square (df = 4; α = 0.05):								*9.49*	*9.49*	*9.49*
Similar Recovery Effort										
26-Sep to 29-Sep	2.0	26	62	2	4,870	5,671	15	0.5%	1.1%	13.3%
30-Sep to 04-Oct	2.0	25	67	2	5,860	6,683	8	0.4%	1.0%	25.0%
05-Oct to 09-Oct	2.0	29	95	2	7,652	10,072	17	0.4%	0.9%	11.8%
10-Oct to 13-Oct	2.0	8	36	0	3,117	4,860	6	0.3%	0.7%	0.0%
14-Oct to 17-Oct	2.0	1	22	1	1,401	2,419	5	0.1%	0.9%	20.0%
Chi-Square Test Result:								*7.94*	*3.47*	*2.04*
Critical Chi-Square (df = 4; α = 0.05):								*9.49*	*9.49*	*9.49*
Similar Total Recoveries										
26-Sep to 29-Sep	2.0	26	62	2	4,870	5,671	15	0.5%	1.1%	13.3%
30-Sep to 02-Oct	1.5	19	44	2	4,196	4,791	8	0.5%	0.9%	25.0%
03-Oct to 06-Oct	1.0	16	68	2	4,867	5,961	10	0.3%	1.1%	20.0%
07-Oct to 09-Oct	1.5	19	50	0	4,449	6,003	7	0.4%	0.8%	0.0%
10-Oct to 17-Oct	4.0	9	58	1	4,518	7,279	11	0.2%	0.8%	9.1%
Chi-Square Test Result:								*7.91*	*9.02*	*2.51*
Critical Chi-Square (df = 4; α = 0.05):								*9.49*	*9.49*	*9.49*

[a] Excludes one disk tag recovered on the spawning grounds less than 5-days after release.

[b] No spawning ground surveys during the initial recovery period at the enumeration fence.

Appendix 10b. Incidence of disk tags in sockeye salmon recovered at the Stellako River enumeration fence, by recovery period and sex, 1994.

Recovery period	Number of surveys	Carcasses recovered with disk tags [a]			Total recovery			Disk tag incidence		
		Male	Female	Jack	Male	Female	Jack	Male	Female	Jack
Similar Recovery Periods										
01-Sep to 22-Sep	22.0	0	10	0	377	827	1	0.0%	1.2%	0.0%
23-Sep to 27-Sep	5.0	17	7	1	2,430	1,912	9	0.7%	0.4%	11.1%
28-Sep to 02-Oct	5.0	53	44	1	6,929	3,336	11	0.8%	1.3%	9.1%
03-Oct to 07-Oct	5.0	21	39	0	5,204	4,168	8	0.4%	0.9%	0.0%
08-Oct to 12-Oct	5.0	10	16	1	2,002	2,654	13	0.5%	0.6%	7.7%
13-Oct to 17-Oct [b]	5.0	0	0	0	0	0	0	-	-	-
Chi-Square Test Result:								*9.60*	*16.26*	*0.97*
Critical Chi-Square (df = 4; α = 0.05):								*9.49*	*9.49*	*9.49*
Similar Total Recoveries										
01-Sep to 27-Sep	27.0	17	17	1	2,807	2,739	10	0.6%	0.6%	10.0%
28-Sep to 30-Sep	3.0	25	14	1	4,008	1,786	8	0.6%	0.8%	12.5%
01-Oct to 03-Oct	3.0	32	34	0	4,211	2,272	6	0.8%	1.5%	0.0%
04-Oct to 06-Oct	3.0	16	28	0	3,279	2,724	4	0.5%	1.0%	0.0%
07-Oct to 12-Oct	6.0	11	23	1	2,637	3,376	14	0.4%	0.7%	7.1%
Chi-Square Test Result:								*4.04*	*14.05*	*1.24*
Critical Chi-Square (df = 4; α = 0.05):								*9.49*	*9.49*	*9.49*

[a] Excludes 15 disk tags (5 male and 10 female) recovered on the fence less than 5-days after release.

[b] Fence was removed on 12-Oct; spawning ground surveys continued until 17-Oct.

Appendix 10c. Incidence of disk tags in sockeye salmon recovered on the Stellako River spawning grounds and at the enumeration fence, by recovery period and sex, 1994.

Recovery period	Number of surveys [b]	Carcasses recovered with disk tags [a]			Total recovery			Disk tag incidence		
		Male	Female[a]	Jack	Male	Female	Jack	Male	Female	Jack
Similar Recovery Periods										
01-Sep to 22-Sep [c]	22/0.0	0	10	0	377	827	1	0.0%	1.2%	0.0%
23-Sep to 27-Sep	5/1.0	27	37	2	4,486	4,461	13	0.6%	0.8%	15.4%
28-Sep to 02-Oct	5/2.8	88	120	4	13,939	11,249	30	0.6%	1.1%	13.3%
03-Oct to 07-Oct	5/1.2	47	131	2	12,070	12,732	23	0.4%	1.0%	8.7%
08-Oct to 12-Oct	5/2.8	26	75	1	7,378	10,540	21	0.4%	0.7%	4.8%
13-Oct to 17-Oct [c]	5/2.2	2	25	1	1,592	2,793	5	0.1%	0.9%	20.0%
Chi-Square Test Result:								*18.78*	*10.27*	*1.95*
Critical Chi-Square (df = 5; α = 0.005):								*16.75*	*16.75*	*16.75*
Similar Recovery Effort										
01-Sep to 22-Sep [c]	22/0	0	10	0	377	827	1	0.0%	1.2%	0.0%
23-Sep to 29-Sep	7/2	59	77	3	9,931	8,711	28	0.6%	0.9%	10.7%
30-Sep to 04-Oct	5/2	78	119	3	12,876	10,586	20	0.6%	1.1%	15.0%
05-Oct to 09-Oct	5/2	43	130	3	11,432	14,143	31	0.4%	0.9%	9.7%
10-Oct to 13-Oct	4/2	9	40	0	3,825	5,916	8	0.2%	0.7%	0.0%
14-Oct to 17-Oct [c]	4/2	1	22	1	1,401	2,419	5	0.1%	0.9%	20.0%
Chi-Square Test Result:								*21.19*	*9.35*	*1.94*
Critical Chi-Square (df = 5; α = 0.005):								*16.75*	*16.75*	*16.75*
Similar Total Recoveries										
01-Sep to 28-Sep [c]	28/1.8	39	63	2	6,820	6,816	19	0.6%	0.9%	10.5%
29-Sep to 01-Oct	3/1.2	58	76	2	9,483	7,538	22	0.6%	1.0%	9.1%
02-Oct to 04-Oct	3/1.0	40	67	2	6,881	5,770	8	0.6%	1.2%	25.0%
05-Oct to 06-Oct	2/0.8	14	61	2	5,054	5,820	12	0.3%	1.0%	16.7%
07-Oct to 09-Oct	3/1.2	29	69	1	6,378	8,323	19	0.5%	0.8%	5.3%
10-Oct to 17-Oct [c]	8/4.0	10	62	1	5,226	8,335	13	0.2%	0.7%	7.7%
Chi-Square Test Result:								*19.80*	*8.74*	*2.92*
Critical Chi-Square (df = 5; α = 0.005):								*16.75*	*16.75*	*16.75*

[a] Excludes 16 disk tags (5 male and 11 female) recovered less than 5-days after release.

[b] Days of fence operation/surveys of spawning grounds.

[c] No spawning ground surveys until 26-Sep; fence was removed on 12-Oct.

Appendix 11a. Proportion of the disk tag application sample recovered on the Stellako River spawning grounds, by application period and sex, 1994.

Application period	Disk tags applied [a]			Carcasses recovered with disk tags			Percent recovered		
	Male	Female	Jack	Male	Female	Jack	Male	Female	Jack
Similar Application Periods									
31-Aug to 06-Sep	59	99	7	19	33	1	32.2%	33.3%	14.3%
07-Sep to 12-Sep	81	286	4	29	98	2	35.8%	34.3%	50.0%
13-Sep to 17-Sep	86	272	6	29	99	3	33.7%	36.4%	50.0%
18-Sep to 22-Sep	55	122	1	8	39	0	14.5%	32.0%	0.0%
23-Sep to 01-Oct	47	97	2	4	13 [b]	1	8.5%	13.4%	50.0%
Chi-Square Test Result:							*18.39*	*18.52*	*3.05*
Critical Chi-Square (df = 4; α = 0.005):							*14.86*	*14.86*	*14.86*
Similar Number Of Tags Applied									
31-Aug to 08-Sep	91	201	8	32	64	2	35.2%	31.8%	25.0%
09-Sep to 12-Sep	49	184	3	16	67	1	32.7%	36.4%	33.3%
13-Sep to 16-Sep	61	199	4	19	73	1	31.1%	36.7%	25.0%
17-Sep to 20-Sep	53	145	2	15	52	2	28.3%	35.9%	100.0%
21-Sep to 01-Oct	74	147	3	7	26 [b]	1	9.5%	17.7%	33.3%
Chi-Square Test Result:							*15.95*	*18.42*	*4.25*
Critical Chi-Square (df = 4; α = 0.005):							*14.86*	*14.86*	*14.86*

[a] Corrected for sex identification error; includes 3 males and 3 females which emigrated from the study area.

[b] Excludes 1 tag recovered less than 5-days after release.

Appendix 11b. Proportion of the disk tag application sample recovered at the Stellako River enumeration fence, by application period and sex, 1994.

Application period	Disk tags applied [a]			Carcasses recovered with disk tags			Percent recovered		
	Male	Female	Jack	Male	Female	Jack	Male	Female	Jack
Similar Application Periods									
31-Aug to 06-Sep	57	97	7	3 [c]	4 [c]	0	5.3%	4.1%	0.0%
07-Sep to 12-Sep	81	285	4	13	23 [b]	1	16.0%	8.1%	25.0%
13-Sep to 17-Sep	86	270	6	34	29 [c]	1	39.5%	10.7%	16.7%
18-Sep to 22-Sep	53	119	1	26 [c]	17 [d]	0	49.1%	14.3%	0.0%
23-Sep to 01-Oct	46	96	2	25 [b]	43 [c]	1	54.3%	44.8%	50.0%
Chi-Square Test Result:							*48.60*	*97.54*	*3.66*
Critical Chi-Square (df = 4; α = 0.005):							*14.86*	*14.86*	*14.86*
Similar Number Of Tags Applied									
31-Aug to 08-Sep	89	199	8	6 [c]	8 [c]	0	6.7%	4.0%	0.0%
09-Sep to 12-Sep	49	183	3	10	19 [b]	1	20.4%	10.4%	33.3%
13-Sep to 16-Sep	61	198	4	22	21 [b]	1	36.1%	10.6%	25.0%
17-Sep to 20-Sep	52	143	2	21 [b]	15 [c]	0	40.4%	10.5%	0.0%
21-Sep to 01-Oct	72	144	3	42 [c]	53 [d]	1	58.3%	36.8%	33.3%
Chi-Square Test Result:							*54.80*	*86.99*	*3.66*
Critical Chi-Square (df = 4; α = 0.005):							*14.86*	*14.86*	*14.86*

[a] Corrected for sex identification error; includes emigrants.

[b] Excludes 1 tag recovered less than 5-days after release.

[c] Excludes 2 tags recovered less than 5-days after release.

[d] Excludes 4 tags recovered less than 5-days after release.

Appendix 11c. Proportion of the disk tag application sample recovered on the Stellako River spawning grounds and at the enumeration fence, by application period and sex, 1994 (see appendices 11a-11b for excluded tags).

Application period	Disk tags applied [a]			Carcasses recovered with disk tags			Percent recovered		
	Male	Female	Jack	Male	Female	Jack	Male	Female	Jack
Similar Application Periods									
31-Aug to 06-Sep	57	97	7	22	37	1	38.6%	38.1%	14.3%
07-Sep to 12-Sep	81	285	4	42	121	3	51.9%	42.5%	75.0%
13-Sep to 17-Sep	86	270	6	63	128	4	73.3%	47.4%	66.7%
18-Sep to 22-Sep	53	119	1	34	56	0	64.2%	47.1%	0.0%
23-Sep to 01-Oct	46	95	2	29	56	2	63.0%	58.9%	100.0%
Chi-Square Test Result:							*19.61*	*10.53*	*8.24*
Critical Chi-Square (df = 4; α = 0.05):							*9.49*	*9.49*	*9.49*
Similar Number Of Tags Applied									
31-Aug to 08-Sep	89	199	8	38	72	2	42.7%	36.2%	25.0%
09-Sep to 12-Sep	49	183	3	26	86	2	53.1%	47.0%	66.7%
13-Sep to 16-Sep	61	198	4	41	94	2	67.2%	47.5%	50.0%
17-Sep to 20-Sep	52	143	2	36	67	2	69.2%	46.9%	100.0%
21-Sep to 01-Oct	72	143	3	49	79	2	68.1%	55.2%	66.7%
Chi-Square Test Result:							*16.86*	*12.93*	*4.67*
Critical Chi-Square (df = 4; α = 0.05):							*9.49*	*9.49*	*9.49*

[a] Corrected for sex identification error; includes 3 males and 3 females which emigrated from the study area. Excludes 5 males and 11 females which were recovered less than 5-days after release.

Appendix 12. Proportion of the Stellako River study area recovery sample marked with disk tags, by recovery location and sex, 1994.

Recovery location [a]	Carcasses recovered with disk tags			Total carcasses examined			Disk tag incidence		
	Male	Female	Jack	Male	Female	Jack	Male	Female	Jack
Upper River	14	80	1	6,102	9,068	13	0.23%	0.88%	7.69%
Middle River	22	74	4	5,367	7,069	17	0.41%	1.05%	23.53%
Lower River	53	128	2	11,431	13,568	21	0.46%	0.94%	9.52%
Fence	101	116	3	16,942	12,897	42	0.60%	0.90%	7.14%
Chi-Square Test Results:									
Chi-Square (Stellako River only)							*5.72*	*1.15*	*2.09*
Critical value (df = 2; α = 0.05)							*5.99*	*5.99*	*5.99*
Chi-Square (Fence vs. aggregate river)							*8.40*	*0.19*	*0.47*
Critical value (df = 1; α = 0.005)							*7.88*	*7.88*	*7.88*
Chi-Square (All Areas)							*13.50*	*1.41*	*3.62*
Critical value (df = 3; α = 0.005)							*12.84*	*12.84*	*12.84*

[a] Sections are: Upper River: areas 1,2, and 3; Middle River: areas 4, 5, and 6; Lower River: areas 7, 8, and 9. Excludes disk tags recovered less than 5-days after release.

Appendix 13. Distribution of recovered disk tagged sockeye adults and jacks during the Stellako River study, by sex and tag application date, 1994.

Sex	Application date	Upper River		Middle River		Lower River		Fence	
		No.	%	No.	%	No.	%	No.	%
Male	31-Aug to 06-Sep	5	23%	7	32%	7	32%	3	14%
	07-Sep to 12-Sep	8	19%	6	14%	15	36%	13	31%
	13-Sep to 17-Sep	1	2%	7	11%	21	33%	34	54%
	18-Sep to 22-Sep	0	0%	1	3%	7	21%	26	76%
	23-Sep to 01-Oct	0	0%	1	3%	3	10%	25	86%
Female	31-Aug to 06-Sep	21	57%	7	19%	5	14%	4	11%
	07-Sep to 12-Sep	32	26%	32	26%	34	28%	23	19%
	13-Sep to 17-Sep	21	16%	21	16%	57	45%	29	23%
	18-Sep to 22-Sep	5	9%	12	21%	23	40%	17	30%
	23-Sep to 01-Oct	1	2%	2	4%	9	16%	43	78%
Jack	31-Aug to 06-Sep	0	0%	0	0%	1	100%	0	0%
	07-Sep to 12-Sep	1	33%	1	33%	0	0%	1	33%
	13-Sep to 17-Sep	0	0%	3	75%	0	0%	1	25%
	18-Sep to 22-Sep	0	-	0	-	0	-	0	-
	23-Sep to 01-Oct	0	0%	0	0%	1	50%	1	50%

[a] Section areas are: Upper River: 1-3; Middle River: 4-6; Lower River: 7-9; excludes disk tags recovered less than 5-days after release.

Appendix 14. Proportion of the disk tag application sample recovered in the Stellako River system, by recovery area, sex, and 3 cm increments of nose-fork length, 1994.

Data set	Nose-fork length (cm)	Disk tags applied [a]			Carcasses recovered with disk tags			Percent recovered		
		Male	Female	Jack	Male	Female	Jack	Male	Female	Jack
Spawning ground [b]	37-39.9	0	0	1	0	0	0	-	-	0.0%
	40-42.9	0	0	1	0	0	0	-	-	0.0%
	43-45.9	0	0	0	0	0	0	-	-	-
	46-48.9	0	0	10	0	0	4	-	-	40.0%
	49-51.9	13	67	8	4	20	3	30.8%	29.9%	37.5%
	52-54.9	61	301	0	19	96	0	31.1%	31.9%	-
	55-57.9	123	378	0	28	126	0	22.8%	33.3%	-
	58-60.9	85	112	0	26	37	0	30.6%	33.0%	-
	61-63.9	41	17	0	10	2	0	24.4%	11.8%	-
	64-66.9	4	1	0	1	1	0	25.0%	100.0%	-
	67-69.9	1	0	0	1	0	0	100.0%	-	-
	Kolmogorov-Smirnov 2-sample test D_{max} (continuous data; see text):							*0.066*	*0.062*	-
	Kolmogorov-Smirnov 2-sample test $D_{critical}$ (α = 0.05):							*0.168*	*0.098*	-
Enumeration fence [c]	37-39.9	0	0	1	0	0	0	-	-	0.0%
	40-42.9	0	0	1	0	0	1	-	-	100.0%
	43-45.9	0	0	0	0	0	0	-	-	-
	46-48.9	0	0	10	0	0	0	-	-	0.0%
	49-51.9	13	66	8	5	14	2	38.5%	21.2%	25.0%
	52-54.9	61	301	0	14	39	0	23.0%	13.0%	-
	55-57.9	121	372	0	44	46	0	36.4%	12.4%	-
	58-60.9	85	110	0	29	17	0	34.1%	15.5%	-
	61-63.9	38	17	0	8	1	0	21.1%	5.9%	-
	64-66.9	4	1	0	1	0	0	25.0%	0.0%	-
	67-69.9	1	0	0	0	0	0	0.0%	-	-
	Kolmogorov-Smirnov 2-sample test D_{max} (continuous data; see text):							*0.040*	*0.051*	-
	Kolmogorov-Smirnov 2-sample test $D_{critical}$ (α = 0.05):							*0.160*	*0.138*	-
Total [d]	37-39.9	0	0	1	0	0	0	-	-	0.0%
	40-42.9	0	0	1	0	0	1	-	-	100.0%
	43-45.9	0	0	0	0	0	0	-	-	-
	46-48.9	0	0	10	0	0	4	-	-	40.0%
	49-51.9	13	66	8	9	34	5	69.2%	51.5%	62.5%
	52-54.9	61	300	0	33	135	0	54.1%	45.0%	-
	55-57.9	121	372	0	72	172	0	59.5%	46.2%	-
	58-60.9	85	110	0	55	54	0	64.7%	49.1%	-
	61-63.9	38	17	0	18	3	0	47.4%	17.6%	-
	64-66.9	4	1	0	2	1	0	50.0%	100.0%	-
	67-69.9	1	0	0	1	0	0	100.0%	-	-
	Kolmogorov-Smirnov 2-sample test D_{max} (continuous data; see text):							*0.031*	*0.035*	-
	Kolmogorov-Smirnov 2-sample test $D_{critical}$ (α = 0.05):							*0.132*	*0.088*	-

[a] Corrected for sex identification error.

[b] Excludes 1 disk tag (female) recovered less than 5-days after release.

[c] Excludes 15 disk tags (5 males and 10 females) recovered less than 5-days after release.

[d] Excludes 16 disk tags (5 males and 11 females) recovered less than 5-days after release.

Appendix 15. Sex composition of Stellako River sockeye adults in the disk tag application and carcass recovery samples, 1994. [a]

Recovery Site	Sex	Application sample, by recovery status [b]				Recovery sample, by mark status			
		Sample size	Recovered	Not recovered	Total	Sample size	Marked	Unmarked	Total
Spawning grounds	Male	325	22.2%	29.9%	27.1%	22,900	22.2%	43.7%	43.5%
	Female	873	77.8%	70.1%	72.9%	29,705	77.8%	56.3%	56.5%
	Chi-Square Test Result:				*7.88*	*Chi-Square Test Result:*			*80.15*
	Critical Chi-Square (df = 1; α = 0.05):				*3.84*	*Critical Chi-Square (df = 1; α = 0.005):*			*10.60*
Enumeration fence	Male	320	46.5%	22.6%	27.0%	16,942	46.5%	56.9%	56.8%
	Female	864	53.5%	77.4%	73.0%	12,897	53.5%	43.1%	43.2%
	Chi-Square Test Result:				*50.11*	*Chi-Square Test Result:*			*8.91*
	Critical Chi-Square (df = 1; α = 0.05):				*10.60*	*Critical Chi-Square (df = 1; α = 0.005):*			*3.84*
Aggregate	Male	320	30.3%	23.0%	27.0%	39,842	30.3%	48.5%	48.3%
	Female	863	69.7%	77.0%	73.0%	42,602	69.7%	51.5%	51.7%
	Chi-Square Test Result:				*7.54*	*Chi-Square Test Result:*			*84.72*
	Critical Chi-Square (df = 1; α = 0.05):				*3.84*	*Critical Chi-Square (df = 1; α = 0.005):*			*10.60*

[a] Data are from Table 4.

[b] Corrected for sex identification error.